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Preface

Invertebrate fisheries are of significant scale and value throughout the Pacific, having a landed weight in 1983 (FAO Yearbook of Fishery Statistics, Vol. 56) of 4.9 million t, 13% of the total landed weight of all species combined. The North Pacific had a total landing of 23.6 million t (3.4 million t were invertebrates), 62% of the total landed weight of all species from all regions combined in the Pacific. In the northeast Pacific, major fisheries exist for king, tanner, and Dungeness crabs, and pandalid shrimp, while numerous smaller fisheries exist for molluscs (abalone, geoduck, intertidal clams, oysters, squid, etc.) and echinoderms (sea cucumbers and sea urchins). In British Columbia alone, over 25 invertebrate species from three phyla are exploited, and while most individual invertebrate fisheries are relatively small in comparison to the region's main resource, salmon, invertebrates still include many under- or unutilized species and are identified as growth areas in future fisheries development. Most presently harvested species, finfish or invertebrate, are currently fully exploited and future regional fishery expansion, except perhaps in Alaska, will occur only through fishery enhancement or development of new fisheries.

The diversity of invertebrate species being currently exploited has meant that invertebrate biologists have to deal with a vast array of gear types, fishing strategies, and management schemes. Gear types include trawl (e.g. shrimp, euphausiid), trap (e.g. prawn, crab, lobster), seine (e.g. opal squid), gillnet (e.g. flying squid), dredge (e.g. scallop, some subtidal clams), and hand-gathering (e.g. intertidal clams, geoduck, echinoderms, abalone); fishing strategies include use of divers (e.g. geoduck, echinoderms, abalone), land-based exploitation (e.g. intertidal clams), daily landings (most nearshore species), and long-duration, offshore exploitation, often with at-sea processing (e.g. flying squid, king crab and some scallops). Management schemes include a variety of methods from closely-monitored active management (e.g. most quota fisheries) to passive management, where perhaps only a minimum size limit is established (e.g. most intertidal clams, Dungeness crab). Often assessment and management approaches are adopted from those developed for finfish, and while this has proven a useful first-step, it is now widely recognized that the unique biological characteristics of many invertebrate species (e.g. extremely high fecundity, limited mobility, cryptic behaviour and protandric hermaphrodism) make development of new approaches a necessity. At the very least, the utility of conventional methodology, mostly developed for finfish, needs review and evaluation as to operational application.

Many invertebrates are now considered luxury foods and command high prices, and this has resulted in levels of exploitation in historical fisheries often considerably greater than previously experienced. New fisheries are also being established, and this overall increase in fishing has caused concern among both fishery biologists and managers as to the current state of many invertebrate stocks. In the past, research and management of many invertebrate resources often received minimal attention because of lack of resources or the belief that such fisheries were minor and of little importance. Traditional fisheries assessment and management methods may not now be as useful as in the past for many invertebrate stocks, and new management approaches specifically directed to current exploitation levels are required. There is immediate need for management evaluation in both developing and developed countries, as in both areas fisheries expansion is often occurring at a greater rate than corresponding increases in research or management resources.

The North Pacific Workshop brought together scientists and managers concerned or interested in invertebrates to (1) address issues associated with assessment of resources and (2) discuss and determine if better management advice, applicable to both developed and developing countries, could be formulated. The Workshop focussed on benthic species because of their regional importance and because other workshops have been recently held on the more pelagic species, notably squid and shrimp. It was appropriate that the Workshop was held in Nanaimo under the auspices of the Pacific Biological Station where there is a long history and tradition of developing new approaches to management of marine and aquatic resources. The Workshop was opened by Dr. D. B. Quayle, the Honorary Chairman and an eminent invertebrate scientist on the Pacific coast of North America. Dr. Quayle has had considerable experience with invertebrate fisheries throughout the world, and he stressed the importance of invertebrate fisheries in the Pacific and hoped that when the Workshop was over we would have a better understanding of factors affecting invertebrate resources and the methods used to manage them.

The Workshop was jointly sponsored by the International Development Research Centre (I.D.R.C.) and the Fisheries Research Branch (F.R.B.), Pacific Region, of the Department of Fisheries and Oceans. We extend our sincere appreciation to both organizations for their support and in particular to Dr. R. J. Beamish (F.R.B.) and Drs. W.H.L. Allsopp, R. Buzeta and F. B. Davey (I.D.R.C.) for their support. We are indebted to Malaspina College in Nanaimo for the use of their facility for the technical sessions. Many people contributed to the Workshop but in particular we would like to thank Marlaine Brown, Susan Strasdine, Kelly Francis and Dwyn Auterson for their untiring and devoted efforts in making the Workshop a success. Finally, we extend our thanks to participants and to all who attended. We trust that everyone at the Workshop benefited from our deliberations and we hope that this Workshop will be the forerunner of continued opportunities for Pacific invertebrate biologists to present results and exchange views in a common international forum at regular intervals.

G. S. JAMIESON AND N. BOURNE

INVERTEBRATE MANAGEMENT — AN INTERNATIONAL PERSPECTIVE

Bivalve Fisheries: Their Exploitation and Management with Particular Reference to the Northeast Pacific Region

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The number of bivalve species in the world is approximately 7 500 but only about 1% of these species were harvested in commercial fisheries in 1980; 38% of reported landings were clams, 31% oysters, 19% mussels and 12% scallops. The Orient (Japan–China–Korea) produced 42% of reported bivalve landings, North America 27%, Europe 19% and southeast Asia and Indonesia 9%; landings from other areas were minor. Compared to world production, bivalve landings in northeast Pacific fisheries (west coast of Canada and the United States) were small, 1.3% of world bivalve production, but fisheries are nevertheless regionally important. Oysters were the dominant commercial bivalve harvested in the northeast Pacific (74%) followed by clams (20%) and scallops (6%). Fisheries for bivalve resources are diverse and range from those that require high capital investment and large boats with sophisticated gear to artisanal fisheries requiring only a stick or bare hands for harvesting. Management of bivalve resources frequently presents different problems from those encountered in management of other aquatic resources.

Many bivalve species are suitable for aquaculture; over half the world's bivalve production is from culture or enhancement operations. Although management of wild stocks is important, they are often fully exploited, and it is suggested that more effort should be devoted to bivalve culture in both developed and developing countries since it is a practical method of increasing production.

Le nombre d'espèces de bivalves dans le monde est d'environ 7 500, mais environ 1 % seulement de ces espèces ont été exploitées à des fins commerciales en 1980; 38 % des débarquements signalés étaient constitués de palourdes, 31 % d'huîtres, 19 % de moules et 12 % de pétoncles. Les débarquements signalés de bivalves se répartissent comme suit : 42 % viennent de l'Orient (Japon–Chine–Corée), 27 % de l'Amérique du Nord, 19 % de l'Europe et 9 % du sud-est de l'Asie et de l'Indonésie; les débarquements provenant d'autres secteurs ont été faibles. Par rapport à la production mondiale, les débarquements de bivalves provenant de la pêche dans le nord-est du Pacifique (côte ouest du Canada et les États-Unis) ont été faibles, représentant 1,3 % de la production mondiale de bivalves, mais la pêche a été néanmoins importante au niveau régional. Les huîtres ont constitué les principaux bivalves exploités commercialement dans le nord-est du Pacifique (74 %) suivies des palourdes (20 %) et des pétoncles (6 %). L'exploitation des ressources en bivalves est diversifiée, allant de la pêche qui exige un gros investissement de capitaux et de gros bateaux avec des engins perfectionnés à la pêche artisanale qui nécessite seulement un bâton ou les mains nues pour la récolte. La gestion des ressources en bivalves présente souvent des problèmes différents de ceux rencontrés dans la gestion d'autres ressources aquatiques.

Beaucoup d'espèces de bivalves conviennent pour la culture; plus de la moitié de la production de bivalves dans le monde provient d'activités d'élevage ou de mise en valeur. Bien que la gestion des stocks sauvages soit importante, ces derniers sont souvent exploités au maximum et on propose de consacrer plus d'efforts à l'élevage de bivalves aussi bien dans les pays développés qu'en voie de développement puisque cela s'avère une méthode pratique pour augmenter la production.

Introduction

The world's bivalve resources are rich, diverse and occupy a wide range of habitats that extend from oceanic depths to high in the intertidal zone and into fresh water. Environmental niches occupied by bivalves are also varied. Some species burrow into substrates of mud, sand, gravel or wood, others attach themselves to firm substrates while others lie free on the bottom. Populations can be extremely variable and range from a few solitary animals to dense aggregations that form a considerable biomass. Bivalves, particularly those that form large aggregations, support a variety of fisheries throughout the world; most are harvested for food but some are used for jewellery, curios and souvenirs. Fisheries for bivalves are also varied; some amount to little more than collecting a sufficient quantity for the next meal while others are large commercial enterprises that are important to local and national economies. Landings from natural populations may be greatly augmented by landings from active culture operations that exist throughout the world.

In the northeast Pacific, i.e. the west coast of Canada and the United States from northern California to Alaska (Fig. 1), bivalve populations support small but valuable commercial and recreational fisheries that are important to many local coastal communities. As in bivalve fisheries throughout the world, stocks in the northeast Pacific are harvested with a variety of gear and are managed by several methods. A few species are

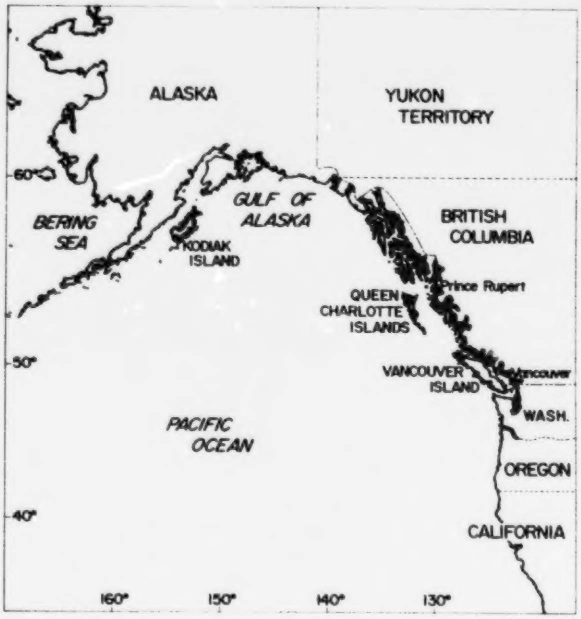

FIG. 1. The northeast Pacific region.

cultured and considerable interest exists here since it offers potential for increasing yields from some areas.

World bivalve fisheries, landings and methods of harvest, are examined briefly, and then bivalve fisheries and management in the northeast Pacific are considered in greater detail. For convenience, bivalves have been divided into four groups; clams, oysters, mussels and scallops, since fisheries and to some extent management strategies fall conveniently into these categories. A further division is between species that are harvested from natural stocks and those that are primarily cultured.

World Bivalve Fisheries

SPECIES

Several estimates have been made of the number of living molluscs and bivalves in the world but Boss (1971) concluded there are about 7 500 bivalve species. Only a small number of these are harvested commercially. In 1980 about 75 species (1% of living bivalve species) provided the major portion of reported landings (Anon. 1981).

Clams

Thirty species, genera or categories of clams were harvested commercially in the world in 1980 (Table 1). Landings of over 10 000 t were reported for nine species and five broader taxonomic categories. The largest landing, 404 014 t, was for "others or mixed clams". The species that provided the largest landing was the manila clam, *Tapes philippinarum*, a species ubiquitous throughout much of the Pacific. Next in magnitude were ocean quahaugs off the Atlantic coast of North America and blood cockles from Asia.

TABLE 1. Species and production (tonnes) of bivalves landed in the world in 1980. Data from FAO 1980 statistics.

Species	Production(t)
CLAMS	
Others and/or mixed clams	404 014
Tapes philippinarum	172 042
Arctica islandica	127 974
Anadara granosa	127 506
Spisula solidissima	91 124
Paphia sp.	35 438
Mercenaria mercenaria	35 381
Anadara sp.	32 427
Protothaca	30 571
Arca	29 925
Cardium edule	27 384
Mactra sachalinensis	21 716
Mya arenaria	21 448
Veneridae	11 441
Panope abrupta	4 582
Cardiidae	4 418
Mesodesma donacium	4 334
Tapes pullastra	4 195
Meretrix lusoria	4 108
Meretrix sp.	2 281
Anadara subcrenata	1 677
Solen sp.	1 543
Saxidomus giganteus	944
Tapes decussatus	776
Protothaca staminea	595
Venus gallinia	341
Tresus capax	156
Siliqua patula	84
Donax sp.	49
Ensis directus	3
Total	1 198 477
OYSTERS	
Crassostrea gigas	498 686
Crassostrea virginica	329 972
Crassostrea sp.	118 422
Ostrea edulis	7 114
Ostrea lutaria	7 025
Crassostrea angulata	3 369
Ostrea sp.	2 608
Crassostrea rhizophorea	2 028
Ostrea chilensis	239
Total	969 463
MUSSELS	
Mytilus edulis	368 798
Mytilidae	73 492
Mytilus crassitesta	70 005
Mytilus smaragdinus	31 386
Aulacomya ater	25 316
Mytilus galloprovincialis	25 075
Mytilus chilensis	10 795
Modiolus sp.	9 065
Mytilus platensis	1 731
Mytilus canaliculus	1 542
Mytilus planulatus	344
*Perna perna*1	
Total	617 550

SCALLOPS	
Placopecten magellanicus	179 041
Patinopecten yessoensis	125 333
Pecten maximum	37 438
Chlamys opercularis	7 906
Pecten meridionalis	5 593
Pectinidae	5 306
Argopecten irradians	3 610
Patinopecten caurinus	2 461
Pecten novaezealandiae	1 420
Total	368 106

Oysters

Boss (1971) lists 50 living species of oysters in the world but only a few are utilized commercially (Table 1). Two species, the Pacific oyster, *Crassostrea gigas*, and the American oyster, *C. virginica*, provided 85% of the world's oyster landings; a grouping "*Crassostrea* sp." represented another 12%. Five other species and the category "*Ostrea* sp." comprise other landings. Most oyster production was from some type of culture operation although the fishery for the New Zealand oyster, *Tiostrea lutria*, is an exception.

Mussels

The world's mussel species total about 250 but landings were reported for only twelve species or groupings in 1980, mostly from culture operations. The blue mussel, *Mytilus edulis*, provided 60% of commercial landings. Five species and one family grouping, Mytilidae, provided another 38% of the landings.

Scallops

About 360 species of scallops exist in the world but three species accounted for 92% of commercial landings in 1980. The largest landings were sea scallops, *Placopecten magellanicus*, off the east coast of North America, followed by the Japanese scallop, *Patinopecten yessoensis*, and the European giant scallop, *Pecten maximus*. Eight species and one family grouping, Pectinidae, provided the total reported landings.

PRODUCTION

Total harvest from the world's aquatic resources in 1980 was about 75 million t annually (Anon. 1981). In 1980 the reported bivalve production was 3 153 596 t, or 4.2% of the world's fisheries production. This was not the total bivalve landings because as in many fisheries, there are known to be significant unreported landings, e.g. artisanal fisheries in many countries and landings in recreational shellfish fisheries. However, these statistics provide the best picture of bivalve landings and the distribution of fisheries throughout the world. They also show that bivalve resources are widely exploited.

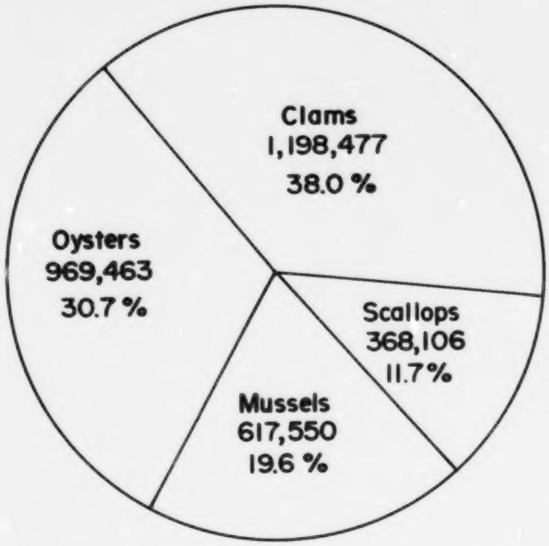

FIG. 2. World production of bivalves (tonnes) in 1980; data from FAO 1980 statistics.

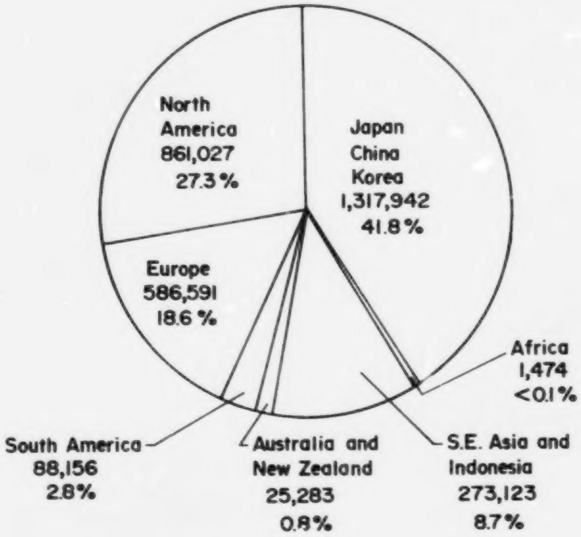

FIG. 3. Production of bivalves (tonnes) by world region in 1980; data from FAO 1980 statistics.

A breakdown of 1980 world bivalve landings shows that 38% (1 198 477 t) were clams, 30.7% (969 463 t) were oysters, 19.6% (617 550 t) were mussels and 11.7% (368 106 t) were scallops (Fig. 2).

If 1980 bivalve production is broken down geographically, the Orient (considered here as Japan–China–Korea) produced 41.8% of reported landings, North America 27.3%, Europe 18.6%, and southeast Asia and Indonesia 8.7% (Fig. 3). Total Asian production, Orient, southeast Asia and Indonesia combined, was 50.5% of world production (1 591 065 t).

The major portion of *clam* landings came from three

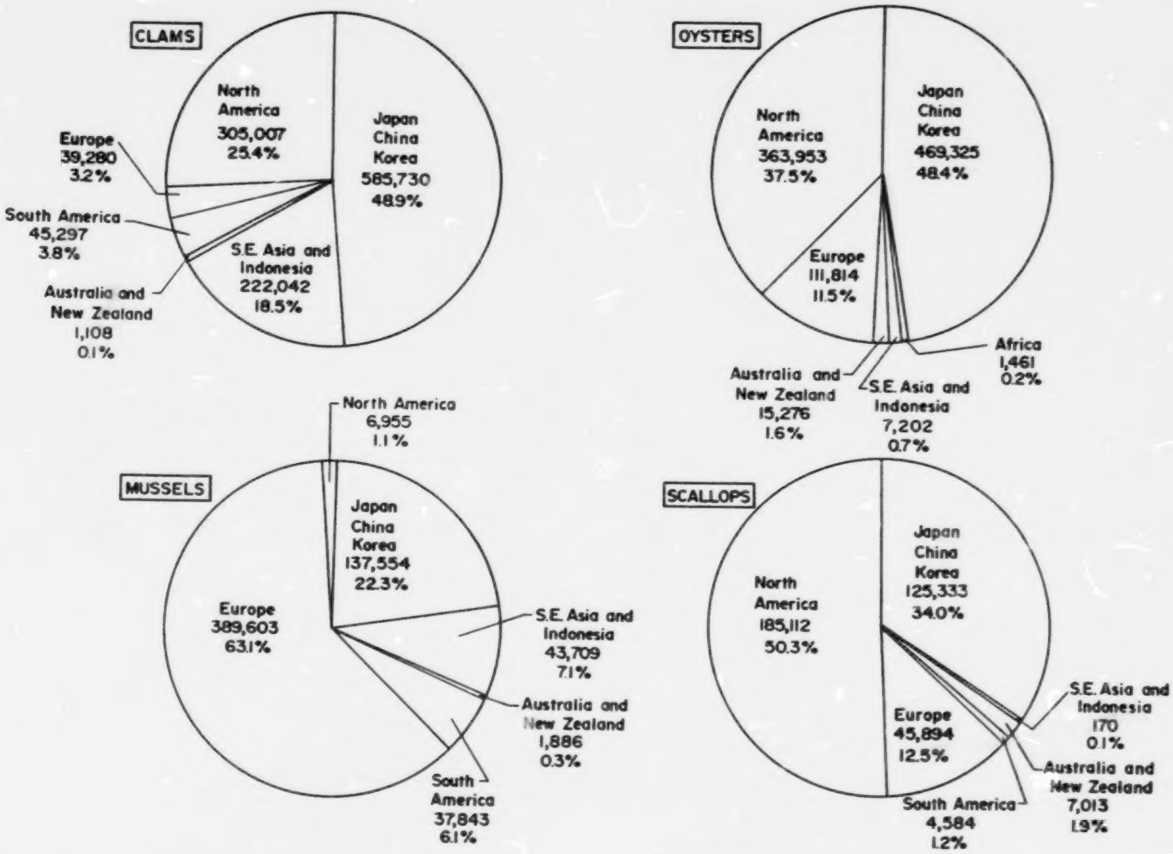

FIG. 4. Production of bivalves (tonnes) by group, (clams, oysters, mussels and scallops) by world region in 1980; data from FAO 1980 statistics.

areas; the Orient 48.9%, North America 25.4%, and southeast Asia and Indonesia 18.5%. These three regions produced 92.8% of 1980 clam landings (Fig. 4). A somewhat similar situation existed for *oysters*; the leading producer was the Orient, 48.4%, followed by North America, 37.5%, and Europe, 11.5%; total production for these three areas was 97.4% of world landings. A different situation existed for *mussels*; most of the 1980 world harvest was from Europe, 63.1%, followed by the Orient, 22.3%; the remainder of the 1980 harvest was primarily from southeast Asia and South America. *Scallop* landings in 1980 were primarily from three areas; North America, 50%, the Orient, 34%, and Europe, 12.5%.

North American bivalve production in 1980 amounted to 803 171 t (Fig. 5); landings by category were clams, 37%, oysters, 40%, and scallops, 23%. Few mussels were landed.

FISHERIES

Fisheries for bivalves are diverse and utilize a variety of gear. Considerable landings are from cultured or enhanced stocks, although from official statistics, it is often difficult to distinguish between enhanced stocks and those that are not. Fisheries for wild stocks are considered in this section; cultured stocks are discussed later.

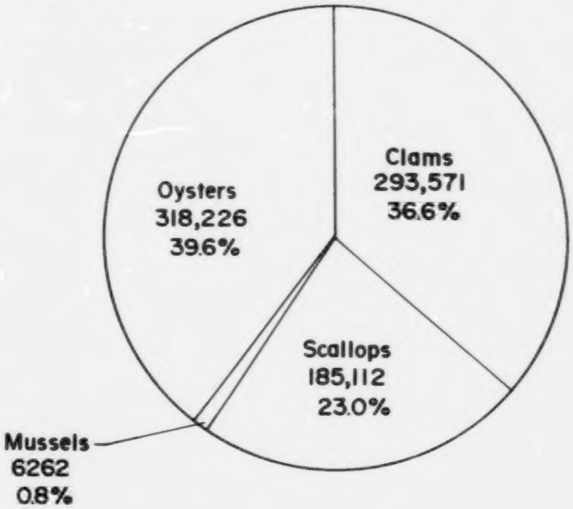

FIG. 5. Clam, oyster, mussel and scallop landings in Canada and the United States in 1980; data from FAO 1980 statistics.

Clams

Clam fisheries are the most diverse of bivalve fisheries and employ a wide variety of harvesting methods ranging from large boats with sophisticated gear to artisanal fisheries that require little more than a stick or bare hands. Surf clam and ocean quahuag fisheries off the east coast of the United States are examples of large clam fisheries which use sophisticated, efficient hydraulic gear that is capable of rapidly harvesting clams in large quantities (Parker 1971; Ritchie 1977; Ropes 1980). Some other subtidal clam fisheries employ smaller boats and dredges; e.g. *Anadara* and *Meretrex* fisheries in Japan (Cahn 1951).

Mechanical clam harvesting gear built in North America to exploit intertidal and subtidal stocks has met with varying success. Hydraulic escalator harvesters have been used effectively in some clam fisheries (Manning 1959; MacPhail 1961; Kyte and Chew 1975) and a hydraulic rake has been used to a limited extent in others (MacPhail and Medcof 1962; Bourne 1967).

A large portion of world clam landings come from the intertidal or shallow subtidal zone, and generally there is little sophistication or degree of mechanization in harvesting. Little equipment is required; a fisherman need only be able to get to a beach and possess some simple digging gear such as a rake or fork. It is generally difficult to obtain accurate landings from such diffuse fisheries.

Oysters

Most of the world's oyster production is from intensive culture or enhancement operations (Korringa 1976a,b; Chew 1982; Ventilla 1984). Culture may be on the bottom or by hanging oysters from rafts and longlines, and frequently involves a considerable degree of sophistication.

One oyster fishery that is not a culture operation is the New Zealand fishery for flat oysters, *Tiostrea lutaria*; wild stocks are harvested from deep water by large boats with dredges (Cranfield 1979). Other fisheries in the world for wild oyster stocks are minor.

Mussels

The world's mussel harvest is mainly from culture operations (Korringa 1976c; Lutz 1980), although there is limited harvest of wild stocks in some areas. Mussels are cultured on the bottom and from rafts and longlines. Many culture operations are large and employ highly developed techniques and gear.

Scallops

Most of the world's scallop fisheries are large boat, high capital-investment fisheries. The largest fishery is for sea scallops, *Placopecten magellanicus*, off the east coast of North America (Bourne 1964). It extends from Newfoundland to the Virginia Capes but is centered in an offshore fishery on Georges Bank and involves both Canadian and American fishermen (Jamieson et al. 1981). Inshore populations exist which are exploited with smaller boats and lighter gear (MacPhail 1954) but landings are less than in the offshore fishery (Jamieson et al. 1981).

In Europe, scallop fisheries are relatively small and involve two species, *Pecten maximus* and *Chlamys opercularis* (Mason 1983). They are generally large boat fisheries with substantial gear and occur in several areas around the United Kingdom and in the English Channel. Attempts have been initiated to culture scallops. Juveniles, produced in hatcheries or caught in collectors, are placed in the natural environment and are either grown to market size under intensive culture operations or are spread on beds to enhance natural populations.

In Japan a single species, *Patinopecten yessoensis*, accounts for virtually all landings (Taguchi 1977; Mottet 1979; Ventilla 1982). Landings now almost equal those of North America; the Japanese fishery is essentially a highly sophisticated culture operation.

Scallop fisheries in Australia and New Zealand are also large boat, heavy gear fisheries (Choat 1960; Sanders 1970). Attempts at culture have been initiated in New Zealand (McKoy 1982).

Northeast Pacific Bivalve Fisheries

SPECIES

The northeast Pacific region has a rich bivalve fauna (Bernard 1983) but as is the case in the rest of the world, only a few species are harvested commercially. Six species comprise most commercial landings: Pacific oyster, *Crassostrea gigas*, and five species of clams: butter, *Saxidomus giganteus*; littleneck, *Protothaca staminea*; manila, *Tapes philippinarum*; razor, *Siliqua patula*, and the geoduck, *Panope abrupta* (Quayle and Bourne 1972; Bernard 1982; Schink et al. 1983). Fisheries for the first four species of clams are mainly intertidal, while the fishery for geoducks is for subtidal stocks by divers using hooka gear (Cox 1979; Harbo and Peacock 1983). Minor landings of two species of horse clams, *Tresus capax* and *T. nuttallii*; cockles, *Clinocardium nuttallii*; and soft-shell clams, *Mya arenaria*, also occur. A small culture industry has recently developed for blue mussels and there are minor landings of four species of scallops; weathervane, *Patinopecten caurinus*; rock, *Chlamys gigantea*; pink, *C. rubida*; and spiny, *C. hastata*. A significant portion of bivalve landings in the northeast Pacific are from two exotic species introduced from Japan, the Pacific oyster and manila clam.

PRODUCTION

Compared to world bivalve landings, bivalve production in the northeast Pacific is small and in 1980 amounted to only 1.3% of world production (Fig. 6). Landings were only 4.6% of the total bivalve production for North America (Fig. 7).

In the northeast Pacific, the Pacific oyster was the major species landed, 73.9%, followed by clams, 19.9%, and scallops, 6.2%, (Fig. 8). No mussel production was reported in 1980. A further breakdown of west coast bivalve landings shows that 83.6% came from the

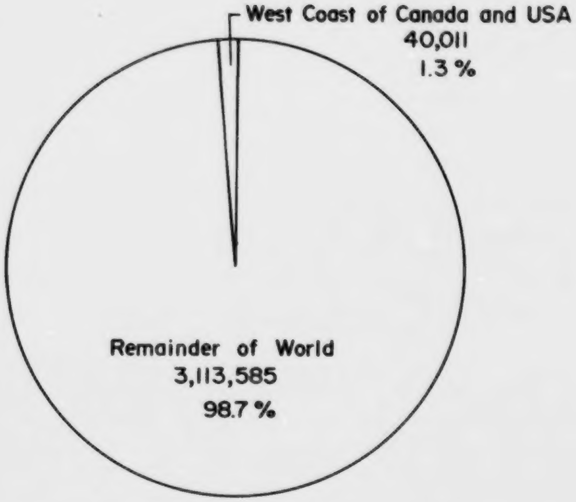

FIG. 6. A comparison of bivalve production (tonnes) from the west coast of Canada and the United States to total world bivalve production; data from FAO 1980 statistics.

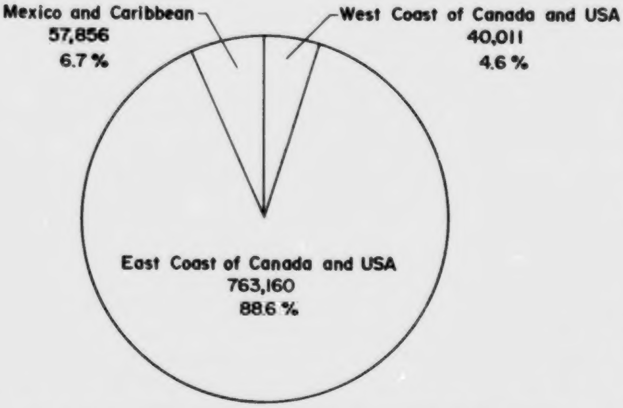

FIG. 7. A comparison of bivalve production in 1980 from three areas of North America; data from FAO 1980 statistics.

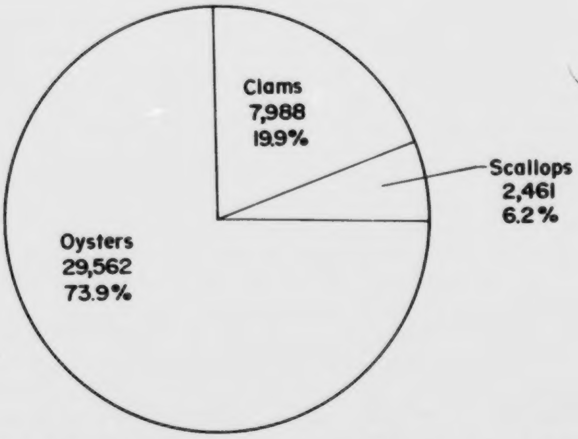

FIG. 8. Production of bivalves (tonnes) by groups from the west coast of Canada and the United States in 1980; data from FAO 1980 statistics.

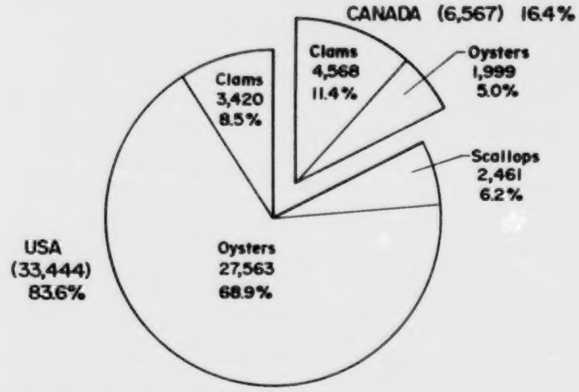

FIG. 9. A comparison of bivalve production (tonnes) by group from the west coast of Canada and the United States.

United States (mostly from the State of Washington) and 16.4% from Canada (Fig. 9). Only clam and oyster landings were reported from Canada although there have been minor landings of mussels and scallops since 1980.

Although bivalve landings from the northeast Pacific are small, resources are widely harvested in commercial and recreational fisheries and are important to some local coastal communities.

FISHERIES

Clams

Commercial fisheries are centered in Washington State and British Columbia (Quayle and Bourne 1972; Schink et al. 1983). Intertidal stocks are harvested mostly by hand digging with forks or rakes. Mechanical harvesters have not found wide acceptance although a few continue to operate in Washington (Kyte and Chew 1975; Goodwin and Shaul 1978; Goodwin and Shaul 1980; Adkins et al. 1983; Schink et al. 1983).

Total clam landings and landings of individual species have fluctuated over the years due to vagaries in market demand, socio-economic factors and abundance (Fig. 10). In Washington, butter and littleneck clam landings have declined slightly and in recent years have been about 115 and 285 t respectively. Landings of manila clams showed a reverse trend and have generally increased in recent years to about 685 t (Schink et al. 1983).

In British Columbia (Fig. 10) there was a general decline in landings of intertidal clams from 1951 to the late 1960's but since then, landings have gradually increased (Quayle and Bourne 1972). Butter clam landings have decreased to about 150 t but littleneck landings have increased since the early 1970's to about 250 t. Manila clam landings are now about 650 t. These fluctuations in landings have generally reflected market demand and socio-economic conditions rather than fluctuations in abundance. A trend in the fishery in the last 10 years has been a shift in landings from butter clams to steamer clams, i.e. littleneck and manila clams, because of consumer demand.

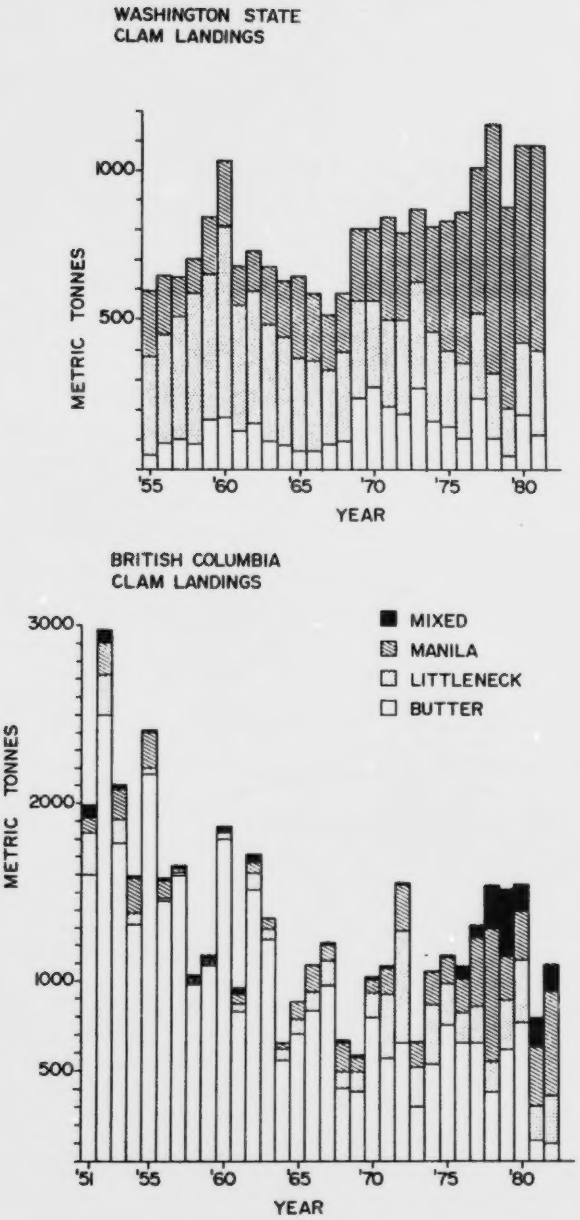

FIG. 10. Recent production of butter, littleneck and manila clams in the state of Washington and British Columbia.

The razor clam is the other intertidal species harvested in the northeast Pacific. In Washington, annual commercial landings were 3 630 t in 1915 (Schink et al. 1983) but have declined to almost nil in recent years, partly because of reduced populations and economic factors but mainly because the resource has been primarily allocated to the recreational fishery. Landings in this latter fishery have been about 1 135 t in recent years (Schink et al. 1983). Commercial landings in Oregon have been about 20 t annually. The British Columbia fishery was never large and landings during the past 10 years have ranged from 27–101 t (Bourne 1979). Extensive razor clam resources exist in Alaska, where commercial landings reached a peak of 2 265 t in 1917 (Schink et al. 1983), but in recent years they have been about 110 t (Nickerson 1975).

Clam landings could be increased substantially in both British Columbia and Alaska as both regions have extensive natural resources. However, there are two major problems: remoteness of many locations from markets, which makes clam harvesting uneconomic, and the presence of paralytic shellfish poisoning (PSP) in varying levels in many bivalves which prevents their utilization as human food (Quayle 1969d; Quayle and Bourne 1972; Schink et al. 1983). Much of the British Columbia coast and all of Alaska is closed to clam harvesting because of PSP; digging is permitted only in specified areas under a carefully controlled monitoring system.

The other major clam species harvesting in the northeast Pacific is the geoduck, which is mainly a subtidal bivalve. For many years they were harvested only in a small recreational fishery but in 1970, a commercial fishery developed in Washington State that spread to British Columbia in 1976. In Washington the fishery is in the Puget Sound area; in British Columbia it is mainly in the southern part of the Province but is expanding into more northern areas. Fisheries are entirely for subtidal stocks and are carried out by divers using hooka gear. A jet of water is used to loosen the sediment around the clam, which is then pulled out by hand (Cox 1979; Harbo and Peacock 1983).

Geoduck landings in Washington increased rapidly to a peak of 3 900 t in 1977 but in recent years have been about 1 950 t (Schink et al. 1983). In British Columbia landings increased rapidly to about 3 000 t in 1982. A quota, about 1.5% of the standing stock, is used to regulate landings (Bernard 1982; Harbo and Peacock 1983).

Extensive surveys have been carried out to assess subtidal clam resources off the outer Pacific coast from California to Alaska to determine if populations exist similar to surf clam and ocean quahaug resources off the Atlantic coast, but results have been disappointing. Few clams of any species were found in most surveys (Quayle 1960, 1961; Hitz 1970; Kessler and Hitz 1971). The most promising find to date has been an extensive population of the pink neck clam, *Mactromeris (Spisula) polynyma*, in the Bering Sea (Hughes and Bourne 1981). It is estimated the annual sustainable yield from this population could be 8 600–11 340 t but no attempt has yet been made to harvest this resource.

Oysters

In the northeast Pacific, oyster production is based almost entirely on culture of the Pacific oyster, *C. gigas*. The main industry is in Washington State, where landings were 24 000 t in 1980 (77% of Pacific coast landings; Beattie et al 1982). California produced about 3 600 t (13%) and British Columbia and Oregon each about 5% of west coast production. In British Columbia all landings are from the southern part of the Province (Quayle 1969b). Production in both Washington and British Columbia has declined in recent years, mostly because of pollution, poor farming practices and socio-economic factors.

Mussels

Minor quantities of wild mussels, mostly *M. edulis* but some *M. californianus*, have been harvested irregularly in the northeast Pacific; the fishery amounts to little more than pulling mussels off pilings, rocks, etc. by hand. A culture industry for *M. edulis* is developing on the Atlantic coast of North America and has recently begun on the west coast (Incze and Lutz 1980; Waterstrat et al. 1980). Currently, culture operations on the west coast produce about 60 t annually in Washington and 5 t in British Columbia.

Scallops

There is a small scallop fishery for weathervane scallops, *P. caurinus*, on the west coast of North America that is centered in Alaska. Landings have fluctuated from nil to a peak of 6 970 t since the fishery began in 1967. In 1981 a small, intense fishery occurred off Oregon and 7 620 t were landed, but in the following year landings declined to 680 t (R. Starr, per. comm.). These fisheries use large boats and heavy gear, but are largely part-time fisheries. Landings depend both on scallop abundance and relative success in other fisheries; when other fisheries are prosperous, fishermen tend to not harvest scallops.

Minor landings of pink, *Chlamys rubida*, and spiny scallops, *C. hastata*, occur in British Columbia, but they are less than 5 t annually.

MANAGEMENT

In the northeast Pacific as elsewhere, resources devoted to research and management of bivalve stocks are usually dictated by economic realities. Some bivalve fisheries, e.g. sea scallop and surf clam fisheries on the east coast of North America, are large and are of considerable economic importance. These fisheries justify extensive research and monitoring by biologists to insure stocks are managed to sustain optimum yields. In the northeast Pacific, bivalve fisheries are mostly small, cottage industries, and are of minor importance when compared to total landed value of fishery products. In 1984 the total landed value of bivalves in British Columbia was $7.9 million, a peak year. This was 3.4% of the landed value of fishery products in the province that year. Under such circumstances, and because of the absence of major management issues, research concern about bivalve fisheries has been limited.

The variety of exploited bivalve species and diversity of fisheries has required development of different approaches to manage them (Hancock 1979). Perceived goals of management policies have been to preserve the marine environment, protect stocks, insure maximum or optimum yields and provide maximum economic return to the industry. No one management method is applicable to all bivalve resources and often many regulations are used to manage a single species. Models used to manage finfish resources have been used to manage bivalve resources, but this seems unsatisfactory because of intrinsic differences between bivalves and finfish.

Management of bivalves presents unique problems. Most bivalves are sedentary, and those that are capable of movement have only limited mobility. They generally have discontinuous and patchy distributions (Davis 1923) which is well demonstrated in northeast Pacific clams (Quayle and Bourne 1972). There are thousands of intertidal beaches of varying sizes along the British Columbia coast which have clam populations whose characteristics can vary considerably within a short distance; significant differences can occur in species and population structure, and in density and growth characteristics (Quayle and Bourne 1972). It would be necessary to sample almost every clam beach to obtain accurate estimates of species abundances along the coast. The patchy distribution of bivalves means that fishing effort is rarely random. Since clams are sedentary the fishery can easily target on areas with dense concentrations. These are exploited until it is no longer economic to do so within constraints of season and size limits, and then the fishery moves to another location.

The potential fecundity of many bivalves is immense; a single female scallop or oyster can produce 100 to 150 million eggs (Quayle 1969b; MacDonald 1984), but large consistent recruitment is rarely the situation because of heavy post-breeding mortalities (Tegelberg and Magoon 1969). The common situation in many bivalve populations is one or two strong year-classes followed by several years of low recruitment and resulting low landings; e.g. butter clams and Pacific oysters in the Strait of Georgia in British Columbia (Quayle and Bourne 1972; Quayle 1969b) and the recent large weathervane scallop population off Oregon (R. Starr, pers. comm.). This can leave managers with the problem of deciding whether to maximize yield from strong cohorts or to try to extend good year-classes for as long as possible to maintain a stable annual landing.

Erratic recruitment has been partly responsible for fluctuations in bivalve landings in the northeast Pacific. However, data do not indicate that fisheries have influenced recruitment magnitude in any population or that fisheries have been responsible for the few bivalve population collapses in the northeast Pacific. Scallop landings declined in Alaska after the fishery began in 1968 to nil in 1978 but since then have increased to early 1970 levels. Initial decline in landings was due to a reduction of virgin population abundance in small, easily located beds, and the recent increase in landings indicates reduced populations can recover. The recent collapse of razor clam populations on heavily harvested Washington State beaches has been attributed to an epidemic disease (Elston and Peacock 1984).

A major reason for fluctuations in bivalve landings in the northeast Pacific has been socio-economic factors, which is evident in the changed species preference in the commercial harvest of British Columbian intertidal clams. Socio-economic factors will probably always have a major influence on landings.

Another regional problem in management of bivalve resources is fishery monitoring. Bivalve fisheries which involve large boats or in which landings are made at central locations can be monitored fairly easily to provide catch and effort data. However, for many bivalve species, landings are irregular, small, and widespread geographically. Easy access to beaches at many locations makes collection of catch and effort information and surveillance extremely expensive and difficult to collect, if not impractical. With the large number of beaches in British Columbia and large number of participants in the fishery (>2500), it is sometimes impossible to determine such basic information as total catch by species, even for relatively large statistical areas.

Management policies often reflect socio-economic conditions. Clam fisheries have traditionally employed many people, particularly those in lower-income brackets, on a seasonal or part-time basis. This has led to development of management policies to maintain traditional employment patterns, even though they may be less efficient than widespread harvesting with mechanical harvesters (Adkins et al. 1983). High employment rather than achieving optimum yield sometimes appears a major goal of management.

A further consideration in management of bivalves in the northeast Pacific is an active and vocal recreational fishery. People often believe it is their inalienable right to harvest bivalves on any beach, and with the popularization of SCUBA gear, to collect bivalves from subtidal populations. Recreational fisheries are valuable but they are diverse and difficult to monitor. Commercial and recreational fisheries sometimes conflict and management policies must be devised to accommodate both fishery types.

Several management approaches, singly or in combination, have been used to manage bivalve stocks in the northeast Pacific.

Unrestricted fishing frequently occurs when fisheries first begin, e.g. the geoduck fishery in British Columbia, or in situations where insufficient resources are available to manage widespread fisheries. If the fishery becomes significant, unrestricted fishing is usually replaced with some type of management regulation.

Size limits are a common management approach. When properly set, they can insure an individual's breeding before harvest and can be designed to permit optimum yield per recruit. They are probably the only regulation that can be readily enforced in many bivalve fisheries in the northeast Pacific. Harvest does not need to be monitored on beaches since size limits can be enforced at central locations, such as processing plants. In general, size limits have proven to be a simple but effective method to manage bivalve resources.

Gear restriction is practised to minimize damage to sublegal animals and the environment. In drag fisheries, size of both drag and mesh and drag design can be regulated. In other fisheries, type of gear which can be used can be restricted, e.g. use of mechanical harvesters on clam beaches. Although some gear may be more efficient and have a reduced manpower requirement, it may damage the environment or be in conflict with policies to provide maximum employment in traditional fisheries, and hence not be accepted (Adkins et al. 1983).

Quotas, trip or area, are occasionally used to manage bivalve stocks. If scientifically based, they should be established after biological assessment of the stock, but such assessments are often expensive to initiate and may involve considerable effort. Quota management may be practical in large fisheries with high capital investment, but it is logistically difficult, if not impossible, to enforce in most small-scale bivalve fisheries, e.g. intertidal clams.

Quotas are commonly used in management of recreational fisheries where they are usually termed catch or bag limits. In a few recreational fisheries, such as the Washington State razor clam fishery, the quota is based on extensive survey of the natural population (Schink et al. 1983). In most northeast recreational bivalve fisheries, quotas are set arbitrarily to provide a mechanism to control the fishery and prevent recreationally caught bivalves entering commercial markets.

Limited entry or controlled effort, often through license limitation, is used to regulate some bivalve fisheries, particularly those involving large boats and high capital investment. It is often used with quotas, such as in the British Columbia geoduck fishery. A difficulty is that although entry into a fishery is limited, fishing power and fishing effectiveness often continue to increase with the result that fishing effort is not stabilized.

Seasonal closures are employed to protect spawning stock or spat settlement, to regulate effort by restricting fishing to particular times of the year for economic reasons (e.g. prohibited harvesting of butter clams in spring and summer in British Columbia), and because of enforcement difficulties.

Reserves, areas where harvesting is permanently restricted, have been established in some places to insure an adequate breeding stock is maintained. This has not been a common practise in the northeast Pacific because there are usually sufficient populations of bivalves in areas that cannot be exploited economically to insure an adequate breeding stock. However, some Pacific oyster breeding reserves have been established in British Columbia and Washington. The fecundity of bivalves is extremely large and it is not generally believed that large broodstocks are required to maintain adequate recruitment.

Biological factors sometimes affect bivalve harvest, e.g. PSP (paralytic shellfish poisoning) and DSP (diarrhetic shellfish poisoning). In British Columbia much of the coast is closed to clam digging because of persistent low levels of PSP and harvest is only permitted under a carefully controlled monitoring system during winter months. In Alaska harvesting of clams is permanently closed because of PSP except in a few local areas (Schink et al. 1983). In Japan, harvest of clams and scallops in some areas is also affected by the presence of PSP and DSP (Ventilla 1983).

Industrial or domestic sewage pollution also affects harvest of bivalves and may result in fishery closure or restriction. In the State of Washington, pollution is a major problem to expansion of the oyster industry (Beattie et al. 1982). In southern British Columbia, over 50 areas have been closed to bivalve harvest because of domestic pollution. Attempts have been made to harvest bivalves from mildly polluted areas and depurate them but this procedure requires close management and inspection to ensure that only safe shellfish are marketed. Bivalves in areas closed because of PSP, DSP or pollution add to the unexploitable brood stock.

In summary, management of bivalve resources involves different approaches, and no one approach is ideal. It is difficult to evaluate fishery impact on future recruitment. Active management is generally easier to institute and enforce in large fisheries where landings are made at a few central locations. In geographically wide-spread fisheries, such as intertidal clam fisheries, extensive data collection and surveillance are typically difficult to effect.

Enhancement and Culture

Enhancement and culture of bivalves presents an opportunity to maximize and even increase production for many growing areas. In many countries, intertidal and immediate subtidal areas are considered "common property resources" and harvesting is open to everyone. In Canada, such areas are referred to as "Crown Land" and bivalves there belong to the first person to harvest them.

In some parts of the world, private ownership of growing areas is permitted. Private ownership usually involves minimum surveillance by managing agencies and is a practical management method for sedentary intertidal species. Owners usually try to manage their area to achieve maximum profit. Private ownership of molluscan shellfish growing areas is permitted in the State of Washington, where it has been instrumental in maintaining high yields (Beattie et al. 1982; R. Burge, pers. comm.), and is well developed in Japan (Mottet 1980a). It has been recommended for consideration in British Columbia (Pearse 1982).

Over half the world's reported bivalve production is from some type of culture or enhancement operation and bivalve culture is widely practised in many developing countries (Davy and Graham 1982). The advantages of culture over harvest of wild stocks have been described (Bardach et al. 1972; Chew 1984) and need not be discussed here in detail. Bivalves have unique characteristics that make them well suited for culture. Many species are sedentary. Seed (juveniles) can be obtained reasonably inexpensively from natural sources or produced in hatcheries, and can be grown to commercial size on natural foods.

Recruitment in many natural bivalve populations is erratic. With culture, it is possible to consistently achieve maximum production from an area and be less influenced by the effects of poor recruitment. With an enhanced, stable production, market development is facilitated.

Greater emphasis on culture is advocated to increase bivalve production in the northeast Pacific. Although oyster production has declined in recent years it could be greatly increased (Quayle 1971). A mussel culture industry is developing and could expand significantly with adequate research and development (Waterstrat et al. 1980). Clam culture, particularly manila clam culture, has potential (Mottet 1980b; Anderson et al. 1982). The State of Washington is investigating the possibility of razor clam and geoduck culture (Chew 1984) and the feasibility of scallop culture is being studied in British Columbia.

Bivalve culture has not developed as quickly as might be expected in the northeast Pacific primarily because of economic factors and this is seen in the oyster industry (Anon. 1977; Chew 1982). However, culture provides an alternative method of production and with adequate research and development it could become much more attractive economically to the industry. Further, culture provides a method to increase production in areas where wild stocks are currently fully exploited. In the future it is anticipated that bivalve culture will become increasingly important in the harvest of bivalves in the northeast Pacific.

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Gastropod Fisheries of the Pacific with Particular Reference to Australian Abalone

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Gastropod fisheries are confined to inshore waters predominantly in temperate zones and, apart from the whelk and periwinkle fisheries of northwestern Europe, located around the Pacific Ocean. World production gradually increased during the 1970's; however, it constitutes only 0.1% of the world's total fish catch and less than 2% of the total mollusc production. Abalone and top shell from the northeast Pacific (FAO area 61) comprise 20% of the total catch; abalone fisheries in Australia (15%) and concholepas fisheries in Chile (35%) dominate gastropod landings.

Commercial fishing for abalone began in Japan 2000 years ago, in North America about 1850, and in Australia in 1963. Technological advances have tended to result in long-term stock reduction. Significant research on population dynamics and management in Japan, Australia, Canada, Mexico, and New Zealand indicates abalone are relatively slow growing (*K* about 0.2) with low natural mortality (*M* about 0.2) and highly fecund. Various techniques, including limited entry and minimum size, have been used to manage stocks, but stock and recruitment relationships are not well understood. Aquaculture-based reseeding programmes and habitat expansion have been widely used in Japan and Korea and are under trial in California, Mexico, and Australia. The Japanese programme has not resulted in an increase in total production. The limited capacity for animals to redistribute the population renders stocks that are sequentially heavily harvested apparently vulnerable to recruit over-fishing. Early signs of this situation can be masked by aggregating catch and effort data from a number of fishing areas. In some fisheries, animals may not have sufficient random distribution to rely on catch per unit effort as an index of stock density.

La pêche de gastropodes est limitée aux eaux côtières des zones tempérées et, à part de la pêche du buccin et du bigorneau dans les eaux européennes nord-ouest, s'effectue dans l'océan Pacifique. Dans les années 70, la production mondiale a graduellement augmenté quoiqu'elle ne représente que 0,1 % des prises mondiales totales de poisson et moins de 2 % de la production totale de mollusques. L'ormeau et la troche capturés dans le Pacifique nord-est (zone 61 de la FAO) et l'ormeau pris en Australie constituent respectivement 20 % et 15 % des prises totales; les captures de conques au Chili (35 %) dominent les débarquements de gastropodes.

La pêche commerciale de l'ormeau est née au Japon voilà 2 000 ans; en Amérique du Nord et en Australie, elle a débuté respectivement vers 1850 et 1963. Les poussées technologiques ont entraîné une baisse à long terme des stocks. D'importantes recherches sur la dynamique des populations et la gestion menées au Japon, en Australie, au Canada, au Mexique et en Nouvelle-Zélande révèlent que l'animal grossit lentement (*K* d'environ 0,2), possède un faible taux de mortalité (*M* d'environ 0,2) et est très fécond. Diverses techniques, y compris un accès limité et une taille minimale, ont été utilisées pour la gestion des stocks, mais on comprend mal la relation entre le stock et le recrutement. Au Japon et en Corée, des programmes d'ensemencement de larves produites par des établissements aquicoles et le développement d'habitats ont été beaucoup utilisés; ils font l'objet d'essais en Californie, au Mexique et en Australie. Toutefois, le programme japonais n'a pas entraîné un accroissement de la production totale. La capacité limitée de redistribution de la population montrée par les animaux rend les stocks fortement exploités en ordre séquentiel en apparence vulnérables à la surpêche des recrues. Les premiers signes de cette situation peuvent être masqués par le regroupement des données sur les prises et l'effort recueillies dans un certain nombre de zones de pêche. Dans certaines pêcheries, la répartition des animaux peut ne pas être suffisamment aléatoire pour pouvoir compter sur les prises par unité d'effort comme indice de la densité du stock.

Introduction

The easy accessibility in shallow water of some large gastropods such as abalone (common name for members of the family Haliotidae) has resulted in long established fisheries in a number of countries bordering the Pacific. Abalone and the turban or top shell (*Turbo* spp.) are the most important and were used for food by Asian immigrants to North America and Australia in the mid-19th century. Dried abalone from California and Mexico was exported to China for most of this century. Prior to 1960, Japan was also an exporter of dried abalone to China; however, as domestic demand grew, local stocks could no longer satisfy the demand. This led to over-fishing of some Japanese stocks and importations from fisheries in the southern hemisphere. The Japanese industry responded by seeking local alternatives — predominantly the turban shell, and also a major programme to increase stocks by habitat expansion and supplementing recruitment with juveniles reared in government hatcheries. Major abalone fisheries are in the southern hemisphere. Modern North American fisheries arose from activities of Chinese and then Japanese divers in southern California in the 1950s and around the Coronada Islands in Mexico (Cox 1962). Much earlier, abalone of this region were important in both the diet and culture of indigenous people of the area (Cox 1962) and appear to have been harvested as early as 5000 B.C. The inability of current stocks to meet the demand for abalone steaks has now resulted in United States imports of frozen abalone from Australia. Mexican abalone dominated the market for canned product until the 1970s, but it has now been supplanted by Australia.

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In South America the loco, *Concholepas concholepas*, family Muridae is present in coastal waters of Chile and Peru and the flesh closely resembles abalone in appearance (Hancock 1969). The species extends from Lobos de Afuera in Peru (5°S lat.) to Magellan Strait (54°S lat.). The loco, a carnivorous gastropod, occupies a very similar ecological niche to the herbivorous abalone and has similar population characteristics (Castilla 1982).

Fishing Methods

As in many other fisheries, technological developments have transformed the capture of gastropods and subjected limited stocks to excessive levels of fishing effort. The important species all occur close to shore in water rarely more than 35 m deep. When fishermen gathered shells by free diving, fishing mortality remained low, but the introduction of the "hard hat" diving method in Japan, although cumbersome and dangerous, decimated many local stocks. Nonaka and Fushimi (1972) report — "As a result of the use of helmet fishing methods the harvest in 1883 was 131 tons but the catch began to decrease rapidly in the following years, 44 t in 1885 and 5 t in 1901". Since then, the annual catch in that area has exceeded 10 t in only 4 years this century. The introduction of this technique in North America shortly afterwards also resulted in substantial increases in catch, but prior to 1950, classical forms of conservation measures seemed to be adequate to preserve stocks (Bonnot 1948). The development of wet suits and mouthpiece regulators during the 1950s allowed the new recreation of scuba diving to prosper. This equipment is also widely used in commercial fisheries and has led to a marked increase in fishing effort.

Concern for new, "too efficient", harvesting methods naturally led to many restrictions in fishing method: e.g. in Japan, although the traditional ama (both men and women divers) began using goggles in about 1970, diving masks were not permitted in Mie Pref. until 1939 (Ino 1980). In Australia, participants in the new sport of scuba diving found that they could be paid for collecting abalone, then known by the traditional name — mutton fish; and this initiated a new commercial fishery. In North America, the activities of recreational fishermen, already causing concern in 1948 (Bonnot 1948), rapidly expanded as these fishermen, now scuba equipped, moved away from the intertidal area to compete in deeper water with commercial fishermen.

Except in Japan, scuba and later hookah divers took over commercial fisheries. Recently, some Australian divers have used a hydraulically powered stainless steel cage which offers protection and saves energy otherwise used in swimming. However, these cages are cumbersome, subject to mechanical failure, expensive, and so are not in widespread use.

The free swimming diver in neoprene wet suit and "hookah" breathing equipment supported by an assistant above in a tender vessel is the most efficient fishing unit. Such a diver may stay underwater for up to 8 hours a day. Beinssen (1979) calculated that such a diver could search 1196 m^2 per hour and fish 900 m^2 per hour when abalone density is 0.2 per square metre. Hamer (unpublished data) confirmed this figure in separate investigations off New South Wales. Faster growth rates seem to be correlated with high oxygen levels and food availability of exposed coastlines; thus weather provides some protection for stocks and influences the fishing pattern (Harrison 1983).

Commercial Fisheries

Gastropod fisheries contribute little to the total world fish catch, but they are delicacies in many countries and thus attract very high unit prices. Abalone is the third most valuable fishery (in terms of landed value of catches) in Australia and loco the second most important mollusc in Chile, ($15.4 million worth were exported in 1981 (Castilla 1976, 1982). Table 1 shows production levels for the years 1971–81 by country and type.

Japan and Korea

In Japan, abalone harvesting by diving is recorded since 30 A.D. (Ino 1980). Naked divers (ama) maintained this fishery for 2000 years before the introduction of helmet and compressed air diving some time before 1879. Throughout the Meiji era (1865–1912), dried abalone constituted some 80% of Japan's seafood exports.

Ten species of abalone are found in Japan. *H. asinina, H. gigantea, H. sieboldii, H. discus, H. discus hannai, H. diversicolor, H. diversicolor supertexa, H. varia, H. crebrisculpta*, and *H. ovina*. The first and last three are small sub-tropical species of little commercial value. The major commercial species is *H. discus hannai* which is a shallow water species similar to *H. kamtschatkana* found off British Columbia and Alaska (Ino 1980). In Japan it is found in the cooler waters of Hokkaido and northeastern Honshu and Korea. *H. gigantea* is a deeper water species found in southern Japan, and the largest — sometimes reaching 25 cm in length. *H. sieboldii* has a similar distribution but is smaller — maximum length 17 cm occurring in shallow waters (10–25 m). *H. discus* also occurs throughout Honshu and Kyushu and is the shallowest species (0–22 m).

TABLE 1. Gastropod fisheries of the Pacific area. Annual landings in kilotonnes live weight. Based on FAO yearbook of fishery statistics.

	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
Haliotis sp.											
Japan	5.7	5.8	5.8	5.0	5.4	5.7	5.2	5.4	4.9	4.9	4.7
Korea	0.6	1.0	2.4	0.5	0.6	0.6	0.6	0.5	0.7	0.6	0.7
Mexico	6.4	5.4	4.7	6.1	6.4	6.4	6.0	4.6	3.7	2.8	1.8
U.S.A.	1.3	1.4	1.4	1.2	1.0	0.8	1.0	1.2	1.3	0.4	0.7
Canada	0	0.1	0.1	0	0.1	0.3	0.5	0.4	0.2	0.1	0.1
Australia	7.8	7.3	6.2	5.4	5.1	5.2	5.1	5.6	6.1	6.7	7.2
New Zealand	1.5	0.7	0.8	0.4	0.5	0.6	0.8	0.6	0.5	0.7	1.3
Other	—	—	—	—	—	—	—	0.2	0.2	0.1	0.1
Total Abalone	24.4	21.7	21.4	18.6	19.1	19.6	19.2	18.5	17.6	16.3	16.6
Concholepas sp.											
Chile	4.9	6.7	5.4	6.1	9.6	10.0	14.2	12.3	16.6	24.9	17.5
Other Gastropods											
Korea				2.0	1.3	2.1	6.6	3.7	2.1	3.8	4.5
Malaysia		0.4	0.3	0.1	5.0	0.7	2.1	0.5	1.2	2.1	2.2
Peru (includes *Concholepas*)		1.4	1.8	1.6	1.6	2.9	2.7	2.3	3.0	4.3	4.5
Chile								0.7	2.2	4.7	4.2
Total Others		1.8	2.1	3.7	7.9	5.7	11.4	7.2	8.5	14.9	15.4
Total all Gastropods		30.2	28.9	28.4	36.6	35.3	44.8	38.0	42.7	56.1	49.5

The long history of the fishery, the impact of technological developments and prefectural and co-operative based management of this fishery has led to an array of measures designed to conserve stocks and regulate fishing. Gill nets and small beam trawls are used to capture abalone in northern Honshu; hooks, poles, and forked spears in Hokkaido. Total or partial prohibitions on diving equipment, closed seasons, and minimum size of first capture are imposed by Prefectural Governments and fishermen co-operatives. Nonaka and Fushimi (1972) report on management measures in Shizuoka. Catch quotas were imposed in 1953 to divers using diving aids in water deeper than 10 m. Women ama diving in the shallow water were not restricted but their catches were improved by the measures. A minimum size of 12 cm was imposed in 1964 and raised to 13 cm in 1971. Since 1966, catches by helmet and mask divers increased and the average length of abalone in the catch also increased.

Kojima et. al. (1978) studied the fishery in Tokushima Prefecture and reported that yields ranged from 19 to 124 t a year between 1894 and 1962. Increased catches there are due to greater fishing effort. Using the De Lury equation to calculate the catchability co-efficient, *q*, this study reported an instantaneous co-efficient of fishing mortality, *F*, of between 1.8 and 2.5.

Central Pacific

Artisanal fisheries for gastropods occur intertidally in a number of Pacific Islands and archipelagic countries. Lopez (1986) discusses such fisheries in the Philippines that are typical of the whole area. Past commercial fisheries for trochus virtually ended when plastic buttons became common but the species is still lightly exploited for ornamental purposes.

South America

The fishery for Concholepas along the 4800 km coastline of Chile and Peru is now the largest gastropod fishery in the world. Castilla (1982) reports that catches are taken from Lobos de Afuera in Peru to Magellanes at the southern extremity of the continent. Landings increased sharply during the 1950s as the important area around Puerto Montt was developed reaching a peak of just under 5000 t. The major earthquake of 1960 severely disrupted many coastal fisheries, but the catch, after falling to half the previous peak, recovered by 1963 but then slowly declined. This situation led Hancock (1969) to urge an inquiry "to investigate the disturbing trends already in evidence for this valuable species". Following the decline, landings again increased to 6700 t in 1972. However, export demands generated a spectacular increase from 1974 to 1980 when catches leapt from 6000 t to over 24 000 t (FAO 1982).

The adjacent fishery in Peru has also grown in the past decade from 1400 t in 1972 to 4500 t in 1981. (1982 production is reported by FAO to be only 3150 t.) *Concholepas concholepas*, known as caracol and *Fissurella crassa*, lapa, are harvested.

North America

Along the Pacific coast of North America a number of abalone species are exploited from Alaska to the northern extremity of Baja California in Mexico. Cox (1962) reviews the early history of the Canadian, United States, and Mexican fisheries from their prehistoric beginnings through the roles of Chinese, and Japanese fisheries to the immediate post war industry. California has an important recreational fishery (Bonnot 1948, Cox 1962, Cicin-Sain et al. 1977, and Mottet 1978). Abalone are no longer abundant along the southern Californian coast. Pollution has destroyed some habitat as have "high-school biology classes, shell collectors, aquarium enthusiasts, and the general public who indiscriminately overturn rocks in the intertidal zone at every opportunity." (Cox 1962).

From 1916 to 1947 the catch consisted almost entirely of the large red abalone (*H. rufescens*). Pink abalone (*H. corrugata*) then became important, and later the green (*H. fulgens*) and white (*H. sorenseni*) were more heavily exploited. From 1951 to 1968, total catch fell from 1818 to 591 t in 1973 (Burge et al. 1975). Each species in turn declined in response to heavy fishing. Burge reports a 300% increase in the commercial fleet since the 1950s and a 400% increase in "party boat" recreational divers. The Burge study isolated recruitment failure as the major reason for this depletion; minor reasons were pollution, sea urchin competition, and predation. It recommends seeding programmes to accelerate the rebuilding of stocks which is consistent with current Japanese policy.

The fishery in British Columbia is described by Breen (1980). A market in Japan in 1976 stimulated production to rapidly reach a peak; subsequently, catches have fallen to low levels. Breen (1986) reports several recent year-class failures, and as this species is near the extremity of its range in this area, periodic recruitment failure might be expected. Quota management, limited entry, and a minimum size regulation have been applied to this fishery.

H. kamtschatkana extends north from British Columbia to the Aleutian Islands. Koeneman (pers. comm.) reports commercial densities south of Sitka, particularly west of Prince of Wales Island. Native Alaskan tribes maintain a traditional fishery by collection at low tide and diving for food and ornamental use. Commercial fishing began in 1963 but remained insignificant until 1977 when it increased to a peak of 150 t; yield has now declined to 40 t. Management measures include the registration of divers, a minimum size of 95 mm, closed areas (to conserve spawning stock and separate commercial and recreational fishing), and two closed seasons. A guideline harvest range of 34–57 t live weight, half in each season, is now in force. Koeneman (pers. comm.) suggests stocks may now be "faltering" and virgin areas more difficult to find. He believes that the accumulation of stocks which resulted from the eradication of sea otters last century may now decline.

Australia and New Zealand

Abalone have been commercially harvested around Tasmania and eastern Victoria for almost 20 years. During that time, the fishery was continuously monitored in Tasmania, and now offers one of the few examples of a complete set of information covering the development of the fishery from virgin state to harvesting at or near maximum sustainable yield.

Prior to 1963, abalone (*Haliotis ruber* and *H. laevigator*) stocks were almost completely untouched. During the 19th century, there were minor harvests by the Chinese, and the indigenous aborigines lightly exploited abalone in shallow waters prior to white settlement. A small-scale fishery was tried but failed in the 1950s. The recognition of Asian markets and the development of scuba equipment stimulated the modern industry early in the 1960s.

The abalone fishery began in Tasmania in late 1963, but no special licences were required until 1965. A 12.7 cm (5 in.) legal minimum length regulation was enforced in 1964 and divers were required to measure abalone under water and to land their catch alive. During the first few years, the fishery expanded rapidly and in 1967 more than 250 divers were participating. The small fee, low capital investment, and attraction of scuba diving combined with relatively high prices for the product produced rapid and unplanned expansion of the fishery. In 1968, the Government, concerned that development should be controlled, aimed at restraining production to 1000 t of cleaned meat (approximately 3000 t live weight) per year until a better stock assessment would allow establishment of rational management. Three steps were introduced at the beginning of 1969. These were:

1. an increase in the licence fee of $100 per annum;
2. the requirement that licence holders be full-time fishermen;
3. the restriction of licences to those already in the industry.

These measures, together with a substantial drop in prices, resulted in 120 divers being licensed at the beginning of 1969 and establishment of a waiting list for new applicants. These measures were effective in meeting management objectives and production stabilized close to the target level.

In 1973, annual medical examinations were introduced for abalone divers and licence holders were required to be full-time abalone divers, rather than just full-time fishermen. Five special licences were also granted to better exploit abalone resources of the Furneaux Group Islands and to relieve unemployment on Flinders Island. From 1969 to 1973, production was relatively stable and prices increased by 400%. During that time, diving-related illnesses began to cause concern and it was evident that a number of licence holders were not fully utilizing their entitlements to participate in the fishery with the result that fishing effort and production fell. The incentive to dive had declined because of concern by divers for their health and attainment of short-term financial goals. Recommendations were made by the management authority to provide a turn-over of divers and to allow veteran and/or unfit divers to leave the fishery, by allowing those holding entitlements for more than 3 years to transfer, i.e. sell that entitlement to another appropriate qualified diver.

In August 1974, the Government agreed to allow divers to transfer their entitlements to hold a licence to another nominated and suitably qualified person. The objectives were:

1. to ensure higher utilization of limited licences;
2. to encourage veteran divers to leave the fishery and ensure a turnover in persons authorized to exploit the resource;
3. to encourage divers with medical conditions caused or aggravated by diving to leave the industry.

From that time, there has been a steady increase in fishing effort and a substantial increase in production. Interestingly, the catch per diving hour also increased from 55 to 65 kg in the first 5 years, apparently indicating that new divers raised the mean effectiveness of fishermen and/or more productive areas were now being fished. Eight years of increased fishing effort would be expected to depress the catch per diving hour as the density of abalone on the grounds declines.

The increase in fishing effort was small in the first year being only 1500 h, but grew to 6000 h in 1976, 8000 h in 1977, 13 000 h in 1978, and 12 000 h in 1979. Using the mean catch per unit effort for these years, this increase in fishing produced a net increase in catch of over 2500 t in these 5 years. The mean annual catch before licences were transferable was 2100 t; in the 8 years that followed, it exceeded 3000 t.

The combination of high prices and flexibility engendered by allowing licences to be transferred has therefore resulted in additional catches worth $33 million at 1981–82 values over the period 1974–75 to 1981–82.

The additional investment by the industry in transferring (i.e. unrestricted purchasing) entitlements is more difficult to estimate; however, it appears to have amounted to between $6 and $6.5 million in 1982 dollars or $800,000 a year.

From the beginning of 1981, the Tasmanian Government has applied a new system for collecting resource rent from this fishery. Whilst the rent will continue to be collected through annual licence fees, the amount of the fee will be based on the current annual value of the fishery. From the 1983 licence year the fee will be 1.5% of the mean value of the fishery over the past 3 years adjusted for inflation.

Development of fisheries in the other Australian States follows a similar pattern. New South Wales was slower to introduce licence limitation (not until 1980). Licences became fully transferable in South Australia in 1980 and were to become so, under strict controls, in Victoria in 1984, but are not "saleable" in New South Wales. Divers in South Australia may use relief divers for up to 21 days a year. All States have rigidly enforced minimum size regulations and all abalone must be landed in the shell. The fisheries are highly profitable (Harrison 1983) and most States collect resource rent through licence fees based on a percentage of gross value of the catch.

The fishery has been subject to a broadly based research programme since it began in 1964. The South Australian Department of Fisheries has concentrated on the biology and ecology of *H. laevigeta* (Shepherd 1973) and in conjunction with the Commonwealth Scientific and Industrial Research Organisation (CSIRO) population biology of *H. laevigeta* and *H. ruber* (Shepherd et al. 1982; Shepherd and Hearn 1983). CSIRO Division of Food Research has intensively studied the biochemistry and food technology of Australian abalone (James and Olley 1970, 1971; Olley 1976; Olley and Thrower 1977; Doe et al. 1973; Young et al. 1973; Young and Olley 1974).

The fisheries biology of *H. ruber* has been studied in New South Wales, in Victoria by Beinssen (1976) and in Tasmania by the author. In Tasmania, each diver submits a monthly return indicating his fishing activities on each day in terms of fishing area, catch, and time spent diving. The State is divided into 49 fishing areas and length frequency distributions are obtained monthly from the important areas. Comprehensive fisheries statistics have been collected from the Tasmanian fishery since 1964.

To date no effective means of aging abalone has been found; thus stock assessments have mainly concentrated on an analysis of changes in catch and effort with age distribution being derived from a growth curve.

Harrison (1983) reports that diving efficiency increased with time and has adjusted the unit effort (an hour spent under water by a diver) to account for this change in efficiency and other improvements in diving operations. This effectively keeps the catchability co-efficient constant and allows estimates to be derived for the maximum sustainable yield by a surplus production model. In the absence of an effective measurement of improved efficiency, a subjective assessment was sought from interviews with divers who have been in the fishery for more than 10 years.

All divers interviewed agreed that there had been a substantial increase in efficiency and there was wide agreement on the factors that contributed to it, viz:

1. Improved diving suits which kept the diver warmer and therefore allowed him to maintain efficiency throughout the diving day.
2. Support for diving operations. As the profitability of diving improved divers employed full time assistants to supervise their tender vessel and lifting the bags of abalone from the water allowed the diver to maintain efficiency over a longer period.
3. Increased Incentive. The availability of new divers to buy their way into the industry naturally provided substantial incentive for these new recruits to work at maximum pressure.

Whilst this is most commonly reflected in increased diving hours, there was general agreement that it also resulted in an improvement in efficiency. There are a variety of ways in which a highly motivated diver can be more productive than one with less incentive. Interestingly, almost all divers believed that this increased incentive also spread to those divers without financial commitments of the new recruits through the naturally competitive nature of fishermen.

4. More skilful new divers. As the cost of entering the fishery rose it became necessary for persons seeking to enter the fishery to demonstrate their likely capacity to be successful divers before they could obtain the necessary finance. This has meant that most new recruits to the fishery are already experienced divers and begin fishing at a higher skill level than new entrants before 1975. In this manner the mean level of skill in the fishery has increased.

During interviews it became evident that most divers now believed that they improved their knowledge of fishing grounds and fishing techniques for 6 to 7 years.

Veteran divers also approach diving in a more professional manner by fishing on a high proportion of days in the year, by having a daily catch target, and by recognizing diving as a business.

Increased incentive is often reflected in divers seeking to take all available legal abalone by measuring each shell underwater. Prior to 1975, most divers judged the length of the shell by eye and left abalone which were near the legal minimum size. The effect of physically measuring abalone to determine whether they are above the legal minimum length is reflected in changes of length frequency distribution of catches. Witherspoon (1975) reviewed this subject and concluded that most divers judged size by eye, and doubtful individuals were not taken. As a result, animals just above the legal minimum length were underrepresented in the catch.

After adjusting effort by a weighting factor (reflecting these changes in fishing power) a simple surplus production model using Fox's method was used to derive maximum equilibrium yields for the whole fishery, the three major zones within the fishery, and the four small areas within zones 1 and 2 which are subject to intensive fishing. This fishing area has expanded due to deeper diving or the discovery of new areas. Within zone 1, the stocks may not yet have reached equilibrium and estimates should be considered as tentative.

It is widely believed that weather, particularly sea conditions, regulates fishing effort in diver fisheries. The author (1983) attempted to quantify this effort by correlating daily meteorological reports with measured diving effort. From this analysis, there is little to suggest that annual catches are significantly affected by departures from the average number of days a year when diving conditions were "good". In Tasmania, catch and effort was much more closely correlated with the price paid to divers for abalone. During the years covered by this analysis, catches were generally well below the equilibrium yield and divers had considerable capacity to expand effort.

Stocks of abalone around the coast of Tasmania appear capable of sustaining an annual catch of 7 million animals, i.e. 3500 t at the current average size. The catch has exceeded this figure in 1980 and 1981 but voluntary catch restraints in response to marketing difficulties in Japan kept production below it in 1982. Improved market conditions in 1983 seem likely to again raise catches above 3500 t in 1983.

Waugh and Hamer (in press) have analyzed the New South Wales fisheries within an economic framework with a view to determining the "best" age at first capture and the "best" level of fishing effort. The analysis is based on the Beverton and Holt yield equation and "best" levels are assumed to coincide with maximum resource rent. Hamer (pers. comm.) has also estimated reef area from aerial photography and used the Deriso model (Deriso 1980) to simulate the abalone population.

A New Zealand abalone species *H. iris* has been traditionally harvested by the indigenous Maori people and has supported a small commercial fishery since the 1960s. Two papers by Sainsbury (1982) report on the population dynamics and management of this fishery.

Management Problems

"Abalone and other gastropod fisheries are highly susceptible to over fishing" — this statement or a similar one occurs constantly in the literature by Castilla (1976), Mottet (1978), and others. Certainly the history of abalone fisheries in Japan, California, Canada, and Mexico show substantial depletion of stocks after heavy fishing. What are the characteristics of this species or the nature of the fishery that may be critical?

Numerous authors have reported that the species are slow growing (*K* about 0.2) and long lived. Natural mortality rates are correspondingly low (about 0.2), fecundity is high, the spawning period is extended and the pelagic larval stage short. These factors promise highly stable populations capable of sustaining substantial fishing mortality. On the other hand abalone is valuable and fishing methods efficient. Beinssen (1976), Forster et al. (1982), and the author have investigated diving efficiency. Australian studies suggest that on some substrata the semi-cryptic nature of some species allows divers to harvest only a small fraction of the total stock. For the less cryptic *H. laevigeta*, Shepherd (1973) and Kojima et al. (1978) report a higher catchability coefficient. Thus the theoretical efficiency of the diving method may be balanced by protection provided by the cryptic nature of some species and the effect of weather and physical demands on the diver in deeper water.

Traditional management response to efficient fishing methods is to restrict effort, control harvest, and limit the efficiency of fishing. Nevertheless, measures such as legal minimum lengths, closed seasons, and areas have not been effective in conserving stocks. The high value of each individual fish encourages fishing stocks down to levels which may threaten recruitment failure (Breen 1980; Castilla 1982). Guzman del Proo (per. comm.) believes the serious decline in Mexican stocks is primarily due to widespread capture of abalone less than the legal minimum length. Conversely, Burge et al. (1975) suggest that the problem in California was caused by size limits for abalone being too high. Breen (1980) calculates that the Canadian legal minimum length may be too high as it exceeds the critical size — at which a single cohort would produce maximum yield. However this assumes recruitment is not closely related to stock size. He believes this is a "poor" assumption and quotes Cincin-Sain et al. (1977) as concluding that the decline in the Californian fishery was due to recruitment failure despite well enforced realistic size limits.

Australia now has considerable experience in the effectiveness of restricting the number of divers as a conservation measure and one must conclude that it is not the whole answer either. It has been effective in developing a very profitable technically advanced fishery and generating considerable resource rent. The majority of divers are skilled and conscious of the need for stock and fishery management. But given sufficient incentive — usually financial — divers are capable of substantially increasing their effort and thus exceed planned catch levels. As already discussed, the financial stimulus created by allowing limited licences to be freely transferable resulted in 125 divers in Tasmania increasing their effort by 50% in 4 years and the catch by 100% in 6 years. (Reducing the number of divers would probably result in individual incomes from the fishery exceeding politically acceptable levels.) Fedorenko and Sprout (1982) and Pearce (1982) recommended an adjustable individual quota system and there seems little doubt that the Australian fisheries must seriously consider such a measure if fishing mortality is to be effectively restrained.

Two factors pose particular problems for the abalone fishery manager — indirect fishing induced mortality and possibly a limited or irregular recruitment at extremities of a species range. Several authors are reported by Mottet (1978) to stress the importance of fishing induced mortality in sub-legal size abalone caused by bleeding from cuts caused by the diver's harvesting tool. The only effective solution to this problem in the commercial fishery is to raise the skill of divers, particularly their ability to judge whether a shell is of legal size. Witherspoon (1975) evaluated this phenomenon with particular reference to length frequency distribution in commercial catches. Another solution is required in areas subject to intense recreational fishing. Habitat disturbances by such non-commercial harvesters may also severely interfere with recruitment.

Abalone may have evolved short pelagic larval stages to ensure that larvae are not swept out to sea and outside their narrow habitat. Consequently high fecundity is necessary to distribute the species along coastlines: whilst this distribution of the species is appropriate for that purpose, it is severely limited as a means of rapidly redistributing recruits throughout a fishery that may extend many hundreds of miles along a continental coastline. So, abalone populations depend on recruitment from mature adults in the same relatively small areas that escape capture. Where an abalone fishery develops in a geographically sequential manner, i.e. heavy fishing of a virgin population then moving a short distance and repeating the operation, recruitment overfishing occurs much earlier in the development of a fishery than might be expected. Any recruitment overfishing would obviously be accelerated if the age of first capture is allowed to fall below the age of maturity. Unfortunately the symptoms may be obscured if fishery statistics are geographically coarse or inaccurate. Thus, as recommended by Fedorenko and Sprout (1982) for the British Columbia fishery, it is desirable to monitor and manage these fisheries in small areas, with fishing mortality in each sub-area regulated to the capacity of the stock to generate recruits. If distribution is significantly aggregated, special measures may be necessary to monitor stock density.

Hancock (pers. comm.) suggests that a system of sequential, or rolling closures of small areas has been successful in restoring stock levels in Western Australia and in the Channel Islands.

While it appears that, for abalone, there is no convincing scientific evidence of a situation where recruitment has been reduced by over-fishing, an understanding of the relationship between stock size and recruitment appears to be crucial to the determination of an appropriate management regime. The role of recruitment in abalone population dynamics is now the focus of research in both South Australia and Tasmania. Sluczanowski (1982) developed a model which suggests that rotational harvesting of reefs would maximize the yield of *H. laevigeta* by increasing total egg production. This strategy may also confine harvesting to times when the density of abalone on the reef is high. Two studies in Tasmania are measuring recruitment to the fishable stock. Aquaculture research in Tasmania is also contributing information on larval and juvenile mortality rates and the role of settlement substrate in recruitment success. White (pers. comm.) has been able to find large numbers of recently settled abalone on coralline algae in the field. A new quantitative method to measure the density of the young-of-the-year is to be published by Prince (Dep. of Sea Fisheries, Tasmania).

The role of the substrate in successful settlement of molluscs has long been recognized. Aquaculture research in abalone has investigated this relationship further with interest in the importance of diatoms and the pedal slime trails. There is now evidence of the importance of encrusting corraline algae in settlement of abalone. Garland (1984) at the University of Tasmania has studied the bacteriological aspect of settlement. He suggests (in press) that a rare bacterium *Moraxella* plays a crucial role in settlement. Abalone, immediately after settlement, feed on the cuticle of the coralline algae and ingest the bacteria which may be a crucial component of the young abalone's intestinal flora.

Shepherd (1973) and Tegner and Levin (1982) suggest that the competitive relationship with the sea urchin is important in abalone population dynamics. This relationship may also play a part in rendering coralline algae attractive to settling abalone larvae. If, as Garland

proposes, it is the bacterial nature of the algal surface which determines successful settlement then this may be a key to the stock and recruitment relationship.

The Role of Aquaculture in Rehabilitation of Depleted Fisheries

If depletion of gastropod stocks is due to lowered recruitment, it is reasonable to assume that a programme of reseeding should assist in rebuilding stocks. The large scale Japanese programmes formalized under the 1974 Law on Coastal Fisheries Ground Management and Development (Sakiyama 1979) and experiments in California and Mexico (Burge et al. 1975) are based on such an assumption. The latter author reports "encouraging success" but catch statistics in Japan show, following an encouraging improvement in the late 1960s, no overall increase in production over the past 12 years despite up to 5 million abalone released each year. Ino (1980), "would like to think that" the cause is the slow growth of the species but is concerned that survival rate of the reseeded juveniles is too low. He urges a programme of cross-breeding and further scientific research into the reseeding programme, particularly into feeding and stimulating food production.

An understanding of the relationship between parental stock and recruitment to the fishable stock would seem to be an essential prerequisite to reseeding depleted areas. The costs of such programmes are high and in the light of Japanese results, benefits are as yet unproven.

Discussion

World supplies of valuable gastropod species are limited — despite a substantial increase in Chilean production — and demand will remain strong, thus encouraging commercial and recreational harvesting. Evidence reported here suggests that an appropriate set of effectively policed minimum size regulation is the cornerstone of managing these fisheries. Despite difficulty in aging individual animals, an appropriate age at first capture and the equivalent size W_c or L_c can be set to maximize yield per recruit. The substantial reduction of population densities recorded in a number of fisheries suggests recruitment over-fishing has occurred. These situations are correlated with technological innovations in some cases and environmental effects in another. Despite high fecundity and low natural mortality abalone have little capacity to redistribute the population after fishing due to limited adult movement, the short pelagic stage of the larvae and discontinuity in the reef habitat. Thus intense sequential fishing along the coast may reduce recruitment particularly if legal minimum size regulations are imposed after heavy fishing has commenced. Effective monitoring of catch per unit effort and mean size of animals in the catch should reveal the development of stock problems if statistical areas are small enough to keep the measure of effort proportional to fishing intensity and counter any significant non-random distribution throughout the area. However, potentially dangerously low levels in the stock can be easily masked if this information is pooled and not examined for each unit (fishing area).

The restoration of depleted areas or the artificial elevation of maximum sustainable yields is attractive to both the industry and management agencies. These programmes require a thorough understanding of the nature of recruitment and the stock and recruitment relationship in particular. It would seem necessary to initially investigate where in the life cycle regulation of recruits occur before initiating such programmes.

Limited entry management has been effective in Australia in maximizing the economic value of abalone fisheries. It has resulted in profitable fisheries, skilled professional divers, substantial resource rent to governments, and some innovation in processing and product development. However, it does not control fishing effort due to the relatively low proportion of total time in the year each diver spends fishing. This latent fishing effort is readily mobilized when incentives to increase catches occur.

Future technological advances such as improved searching techniques or physical, biological or perhaps chemical methods of harvesting could quickly trigger increases in fishing mortality. Future management should be directed towards maximizing diver involvement in the regulation of harvesting in small areas supported by comprehensive monitoring of the population, and stock enhancement based on a thorough understanding of the biological and ecological basis of the recruitment process.

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World Jellyfish and Tunicate Fisheries, and the Northeast Pacific Echinoderm Fishery

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Although jellyfish, tunicate and echinoderm fisheries might be considered exotic, they nonetheless represent ancient near-shore fisheries of some Asian and Mediterranean countries. Moreover, present day import demand in Asian countries has stimulated fisheries elsewhere in developed and developing countries. Available information on the landings and fisheries biology is summarized at either the species, species group, or family level. Japan imports $40–50 million (US) per year of medusae (Family Rhizostomatidae) from southeast Asia, yet the biology of this group is virtually unknown, and no fisheries management information on the resource could be found. Similarly, commercial tunicate (Family Pyuridae) fisheries are poorly covered in the literature although the product is highly prized in such countries as Korea, Japan, Chile, and France. Echinoderm fisheries and their management in the northeast Pacific for the red sea urchin *Strongylocentrotus franciscanus* and sea cucumbers *Parastichopus* spp. are better documented. Urchins have attracted much interest because of their importance to kelp forests as grazers and their harvesting may influence other kelp-associated resources such as abalone, lobster, kelp, and certain finfish.

Bien que la pêche aux méduses, aux tuniciers et aux échinodermes soit considérée exotique, elle représente néanmoins une forme ancienne de pêche pratiquée près de la côte dans certains pays asiatiques et méditerranéens. De plus, la demande actuelle en importation dans les pays asiatiques a stimulé la pêche pratiquée ailleurs dans les pays développés ou en voie de développement. Les informations disponibles concernant les quantités débarquées et la biologie piscatoire sont résumées soit au niveau des espèces, des groupes d'espèces ou des familles. Tous les ans, le Japon importe une valeur de 40 à 50 millions de dollars étatsuniens de méduses (famille des Rhizostomidés) du Sud-Est asiatique, pourtant la biologie de ce groupe est virtuellement inconnue et l'auteur n'a pu trouver aucune information de gestion des pêches concernant cette ressource. De la même façon, la pêche commerciale du tunicier (famille des Pyuridés) est très négligée dans la documentation scientifique même si ce produit possède une haute valeur dans des pays comme la Corée, le Japon, le Chili ou la France. La pêche aux échinodermes et leur gestion dans le Nord-Est du Pacifique pour l'oursin rouge géant *Strongylocentrotus franciscanus* et les holothuries *Parastichopus* spp. est par contre mieux documentée. Les oursins ont pris beaucoup d'intérêt parce que leur importance comme brouteurs des forêts de varech et leur récolte peuvent influer sur d'autres ressources liées au varech comme l'ormeau, le homard, le varech et certains poissons.

Introduction

This review describes three invertebrate fisheries, each with a different characteristic 'mobility' *sensu* Hancock (1979): 'fully mobile' pelagic jellyfish, 'sedentary, attached' tunicates and 'semi-mobile' sea urchins and sea cucumbers. As landings of jellyfish and tunicates have been largely confined to the Pacific, their world fisheries are reviewed. The world echinoderm fishery is reviewed elsewhere (Sloan 1985) and, therefore, a detailed account of only the northeast Pacific echinoderm fishery is provided here.

I recount landings data on these fisheries and discuss biological characteristics of harvested species or species groups at the Family level. While jellyfish and tunicate fisheries are poorly documented and artisanal fisheries, echinoderm fisheries in the northeast Pacific are relatively more capital intensive and better documented. Where management occurs, its biological bases are described and where it does not occur, relevant biological information is nonetheless summarized. None of these fisheries have yet been analyzed to determine optimal harvest strategies, and so this first-ever review on these fisheries is descriptive in nature.

Jellyfish

RHIZOSTOME JELLYFISH

The world jellyfish fishery, with an approximate annual value of $40–50 million (US), occurs mainly for export to Japan (Omori 1978, 1981). It is second in value to other coelenterate (coral) fisheries, especially precious coral (Grigg 1984a,b) and, to a lesser extent, stony coral (Ross 1984). There are at least five commercially exploited jellyfish species, all large, firm-bodied, and in the warm water Family Rhizostomatidae. Recent world landings indicate Thailand and China have been the biggest producers (Table 1). Landings averaged approximately 60 000 t annually between 1975 and 1979 before declining in 1980, and then increasing to ≈ 212 087 t in 1983. This small boat, dip-net fishery is highly seasonal and occurs close to shore. Jellyfish are processed with salt and alum to decrease the 96–98%

TABLE 1. World rhizostome jellyfish landings according to country from FAO Yearbooks of Fisheries Statistics (Anon. 1982, 1983, 1984).

	% world landings according to year					
Country	1978	1979	1980	1981	1982	1983
Thailand	91.8	78.1	17.6	56.2[b]	80.4[b]	81.9[b]
China	5.4	18.5	73.4	35.2	14.2	9.0[c]
Indonesia	2.8	3.4	4.1	4.7	1.6	0.9
Philippines	0.0	0.0	4.9	3.9	0.1	0.1
Malaysia	0.0	0.0	0.0	0.0	3.7	8.1
World rhizostome jellyfish landings[a] total (t)	68 158	70 314	12 261	51 272	127 064	212 087[c]

[a] Landings are live weight (t).

[b] Between 1981 to 1983 their Indian Ocean coast has accounted for 67.5% of annual Thai landings.

[c] Indicated as incomplete estimates by FAO.

water content to ≈ 60–65%. The product, whose major edible component is collagenous connective tissue protein (Kimura et al. 1983), is marketed largely for soupmaking.

The rhizostome fishery has been poorly studied; stock sizes are unknown and little resource management is exercised. Moreover, their biology is not well known and their taxonomy is in disarray (Omori 1981). Harvesting occurs in summer and early autumn in northern latitudes (south Japan) and earlier in the year in more southern latitudes (Malaysia) (Omori 1981). Monsoon winds strongly influence the seasonality of harvesting on southern grounds.

The early life histories (planula to ephyra) of all commercial species are poorly known although they are probably similar to those of other rhizostome medusae (Sugiura 1963; Calder 1982). Jellyfish are usually transported in currents far from their spawning site (Uchida 1954). A life cycle of 1 year seems likely (Omori 1981). Rhizostome jellyfish feed on zooplankton (Phillips et al. 1969) and growth must be extremely rapid, for maximum body size is reached in 1 year. Interannual catch fluctuations can be great, perhaps reflecting either variations in currents or wide oscillations in stock size, situations similar to those in another pelagic invertebrate (squid) resource (Arnold 1979).

The main harvested species is *Rhopilema esculentum*, which reaches a 50 cm bell diameter and a weight of 30–50 kg (Omori 1981). There is a traditional June to October fishery for *R. esculentum* along the South Korea, China, and southwest Japan coasts and a larger, recently established April to October fishery for *R. esculentum*, *R. hispidum*, *Lobonema smithi* and *Mastigias* sp. in Thailand, Indonesia, and Malaysia (S. Chaitiamvong, pers. comm.). In the Ariake Sea, Kyushu, Japan, young *R. esculentum* were found inshore in April–May, adults offshore in August–September, and senescent adults in the offshore deeps in November–December (Omori 1981). Early life stages of *R. esculentum* have been raised in the laboratory and the potential for some individuals to have a greater than 1-year life has been suggested (Jiekang and Gengwu 1983; Jiekang et al. 1984).

There are also cooler water, more northerly commercial rhizostome species such as *Stomolophus nomurai*, found in the Sea of Japan (Uchida 1954). According to Omori (1978) *S. nomurai* occasionally occurs in late summer–early autumn "swarms" that, as in other rhizostomes, may relate to spawning (Hamner and Hauri 1981). *S. nomurai* can have a bell diameter of 1 m and weight greater than 100 kg (Omori 1978).

Being largely a warm water group, rhizostome medusae probably occur in the coastal waters of many developing countries and could support an export fishery in the future. Small boats and simple net gear already used for inshore fisheries would minimize the need for further investment in gear. Processing technology (salting) is labor-intensive, but not sophisticated.

OTHER JELLYFISH

Japanese processors appear interested in exploring other species such as *Aurelia aurita* (Family Ulmaridae), a cosmopolitan temperate water species (Möller 1980a). *A. aurita* is much smaller and its body less firm than that of rhizostome jellyfish. The biology of *A. aurita* is well reported from Europe, Japan, and to a lesser extent in the northeast Pacific. There may be enough biological information to predict stock availability and abundance for what could be a summer-early autumn fishery.

The life cycle of *A. aurita* is well known and usually lasts a year although overwintering ephyrae (Hernroth and Gröndahl 1983) and adults (Hamner and Jenssen 1974; Möller 1980a,b) occur. Adult medusae are abundant (often occurring in swarms) in summer followed by degeneration and die-off after spawning in the cooler months (Möller 1980a,b). Growth is rapid in the summer as juveniles approach breeding size (Hamner and Jenssen 1974; Möller 1980b), feeding on zooplankton and larval fish (Möller 1980a; Bailey and Batty 1983). Harvesting should therefore be around late summer for prespawning adults, when mean size and body quality are prime. Surface water fishing around dusk would be most efficient as *A. aurita* congregates near the surface

TABLE 2. World tunicate landings according to area and species from FAO Yearbooks of Fisheries Statistics (Anon. 1982, 1983, 1984).

Area/Country	Species	% world landings according to year					
		1978	1979	1980	1981	1982	1983
SE Pacific/Chile	*Pyura chilensis*[b]	48.5	48.9	54.4	46.8	67.7	55.8
NW Pacific/South Korea	*Halocynthia roretzi*	49.4	48.5	43.7	51.2	29.6	41.7
Mediterranean/France	*Miocrocosmus sulcatus*	1.9	2.2	1.6	1.7	2.4	2.3
SE Atlantic/South Africa	*Pyura stolonifera*	0.2	0.4	0.3	0.3	0.3	0.2
World tunicate landings[a] total (t)		5466	4143	5419	4852	3997	4227

[a] Landings are live weight (t).

[b] *Pyura praeputialis* is also harvested, in restricted areas, in Chile (Paine and Suchanek 1983).

at this time (Yasuda 1973) because of active upward swimming during the day, which is followed by downward migration at night (Mackie et al. 1981).

A. aurita from southern British Columbia waters are easily harvested in summer but their low connective tissue protein levels yield a poor quality product after processing (Sloan and Gunn 1985).

Tunicates

Tunicate species of the Family Pyuridae are harvested by divers or by hand intertidally in a few widely scattered countries, mostly for local consumption (Table 2). Tunicates are usually boiled or eaten raw after the tunic is removed. Annual world landings, which averaged ≈ 4684 t between 1978–83, have been dominated by South Korea and Chile. Japanese production is not listed by FAO although ≈ 6300 t of *Halocynthia roretzi* were line-cultured in eastern Honshu in 1975 (Mottet 1980). Production in Japan has probably increased since then, although the occurrence of paralytic shellfish poisoning (Nagashima et al. 1984) may affect production by curtailing harvest seasons.

Although the state of the world resource is unknown, relatively low landings suggest underfished stocks or poor export market development. With the exception of South Korean stocks, no published information is available. In South Korea, the harvest of wild *Halocynthia roretzi* was greatly curtailed by an unusually severe mass mortality in the late 1970s. Raft-suspended rope culture was initiated in response to subsequent price increases (Kang et al. 1982; Yoo and Ryu 1982). Early life history research, seed production, and rope culture technology studies on *H. roretzi* have flourished (Pyen et al. 1977; Jang 1979; Kim et al. 1979; Yoo and Ryu 1982). Ironically, the main fouling pest decreasing tunicate culture production is the edible mussel *Mytilus edulis* (Jang 1979; Kim et al. 1979). Optimal site criteria for tunicate culture along the southern coasts of Korea have been described (Kim 1980). Moreover, the seasonal (autumn) mortality phenomenon arising from high summer water temperatures followed by starvation of *H. roretzi* at culture sites has been addressed (Chang et al. 1982). Management of natural *H. roretzi* stocks is not mentioned but there has been an energetic program of mariculture.

Pyura chilensis and *P. praeputialis* in Chile and *P. stolonifera* in South Africa are all large species which form dense intertidal beds on rocky shores (Day 1974; Zamorano and Moreno 1975; Paine and Suchanek 1983). Harvesting in Chile (Hancock 1969; J. C. Castilla, pers. comm.), and probably in South Africa, is for local consumption. Landings since 1945 have steadily increased in Chile where the soft inside portions are mostly eaten raw, although some are canned or smoked commercially (Hancock 1969).

The rapid Korean development in tunicate mariculture suggests a strong market for this product. Tunicates may have potential as an export commodity of mariculture from developing countries. Their early life histories have been extensively investigated, because of their intrinsic zoological interest, and rope culture technology for invertebrates is well developed (especially for bivalves) in many parts of the world.

Northeast Pacific Echinoderms

SEA CUCUMBERS (*Parastichopus* spp.)

Two *Parastichopus* species are harvested along the Pacific coast of North America: *P. californicus* occurs in the shallow subtidal (<100 m) from the Gulf of Alaska to Isla Cedros (Baja California) and *P. parvimensis*, a smaller species, occurs in shallows (<30 m) from Point Conception, California to Point San Bartholme (Baja California) (Brumbaugh 1980; Yingst 1982). Landings of *Parastichopus* spp. in North America were first recorded in 1971, remained low until 1976 (≈ 7 t), peaked in 1983 (772 t) and fell to 156 t in 1984 (Fig. 1). This is a diver fishery, with trawling only in the Santa Barbara Channel, California (McDaniel 1982; McNair 1982). Muscle strips from inside the body wall are supplied to a domestic market or exported to Hong Kong and Japan. Sea cucumber landings in North America have been reported from British Columbia, Washington State, and California.

In the majority of sea cucumber fisheries world wide, the entire body wall is utilized. The world fishery is dominated by Japanese landings of *Stichopus japonicus* followed by tropical species from the Indian and Pacific oceans (Mottet 1976a; Sloan 1985).

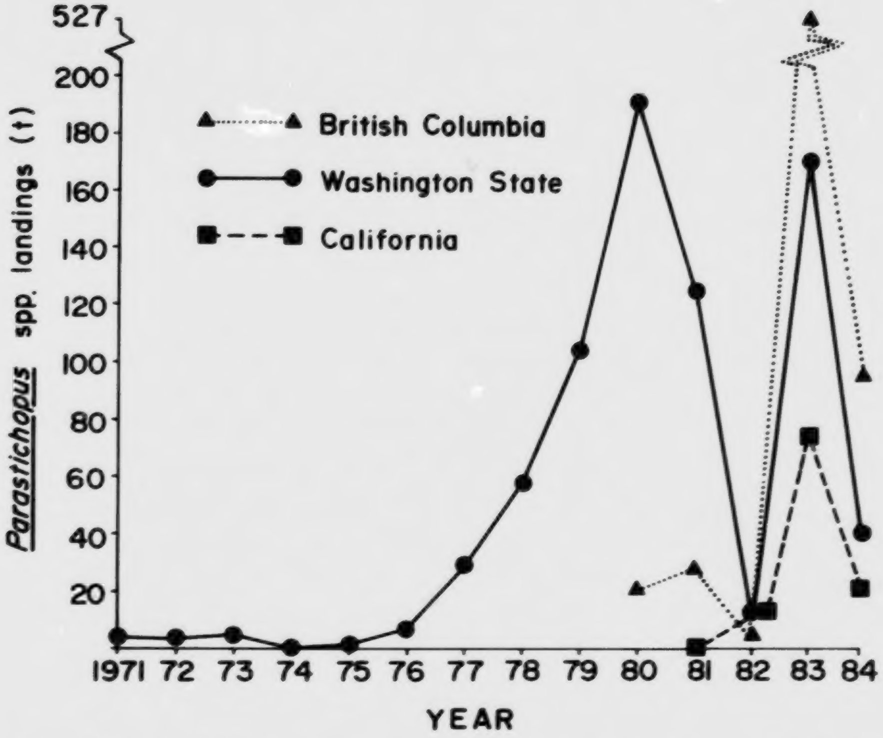

FIG. 1. Landings of *Parastichopus* spp. along the Pacific coast of North America. Data from various regional management agencies.

Harvesting of *P. californicus* in British Columbia began in 1980 and increased strongly in 1983 to 527 t, with 43 vessels reporting landings (Fig. 1). Landings for 1984 decreased to 95 t and will be ≈ 275 t in 1985, due largely to market conditions (R. M. Harbo, pers. comm.). The philosophy of management has been preemptive to limit harvesting of this species whose biology, until recently, was not well known. Prior to 1983, harvesting occurred in the southern Strait of Georgia only. Divers were required to submit detailed harvest logs from the grounds (Harbo 1982). This permitted managers to assess effects of harvesting and review alternate management possibilities. In 1983, fishing was regulated with a special fisheries licence (Z) which embodied most of the original restrictions but allowed harvesting to occur in more areas. This area expansion was to allow increased marketing trials, and it attracted more diving fishermen (R. M. Harbo, pers. comm.). Within designated fishing areas there are no landing quotas nor seasonal closures. Nonetheless, much of the British Columbia coast is still under closure as managers want more biological information before allowing further fishery expansion. Commercial densities are presently >0.25 sea cucumbers m^{-2} and a diver harvests up to 2500 sea cucumbers per day.

The sea cucumber fishery in Washington State was small between 1971 to 1976 and peaked in 1980 (191 t) due in part to the post-1976 decline of the diving sea urchin fishery (Fig. 1; B. Pease, pers. comm.). Landings decreased through 1982, peaked in 1983 (171 t), fell in 1984 (40 t), and will be ≈ 100 t in 1985. Fluctuations are due mostly to market instability rather than stock depletion (B. Pease, pers. comm.). This fishery has few management regulations and neither area nor seasonal closures. There is a seasonal market demand which is low in summer. Managers monitor the fishery through mandatory log books and no research is currently being undertaken.

The California fishery first reported landings in 1981, grew to 74 t in 1983, fell to 21 t in 1984, and will be ≈ 20 t in 1985 (Fig. 1; D. O. Parker, pers. comm.). Harvesting occurs mostly in the Santa Barbara Channel where *P. parvimensis* dominates the catch (McNair 1982). Management is similar to that for other sea cucumber fisheries. There is unrestricted harvesting which is recorded in mandatory log books to provide managers with an indirect stock assessment tool (D. O. Parker, pers. comm.).

Recent progress in understanding the biology of *Parastichopus* species may aid in management of sea cucumber fisheries. *P. californicus* in British Columbia spawns mostly from June to August, followed by an approximately 50–90 day larval life (Strathmann 1978) and subsequent settlement in nursery areas, such as dense mats of filamentous red algae (J. L. Cameron, pers. comm.; Cameron and Fankboner 1986). Size at sexual maturity, which is ≈ 0.5 kg, may be reached in 4 to 8 years (P. V. Fankboner, pers. comm.; Cameron and Fankboner 1986). This is also the size at which they first begin to be fished. The deposit-feeding processes in both juvenile and adult *P. californicus* are discussed in detail by Cameron and Fankboner (1984). Fankboner and his colleagues have found that body wall biomass decreases in most of the population in early autumn due to cessation of feeding and atrophy of the viscera. Whether muscle strips on the inside of the body wall are also affected at this time is not yet clear.

Some data on the life history and population dynamics of adult *P. parvimensis* are available (Yingst 1976, 1982; Muscat 1982, 1983). *P. parvimensis* spawns from May to June and settlement occurs between September and October among kelp holdfasts for protection from fish predators (Muscat 1983). Muscat also reports on morphometrics, distribution, activity patterns, and ecological effects of feeding by *P. parvimensis*.

SEA URCHIN (*Strongylocentrotus franciscanus*)

Landings and Fisheries Development

Along the Pacific coast of North America, only red sea urchins, *Strongylocentrotus franciscanus*, are harvested. This is a large species (to 160 mm test diameter) distributed from northern Japan through Alaska to Baja California (Durham et al. 1980). Red urchins are harvested by divers in a seasonal fishery for their roe (Kramer and Nordin 1975) which is exported to Japan mostly in the fresh, raw state (Mottet 1976b). Total commercial North American landings of *S. franciscanus* increased rapidly in the first decade to 11 676 t in 1981 and have since declined to ≈ 8909 t in 1984 (Fig. 2). In

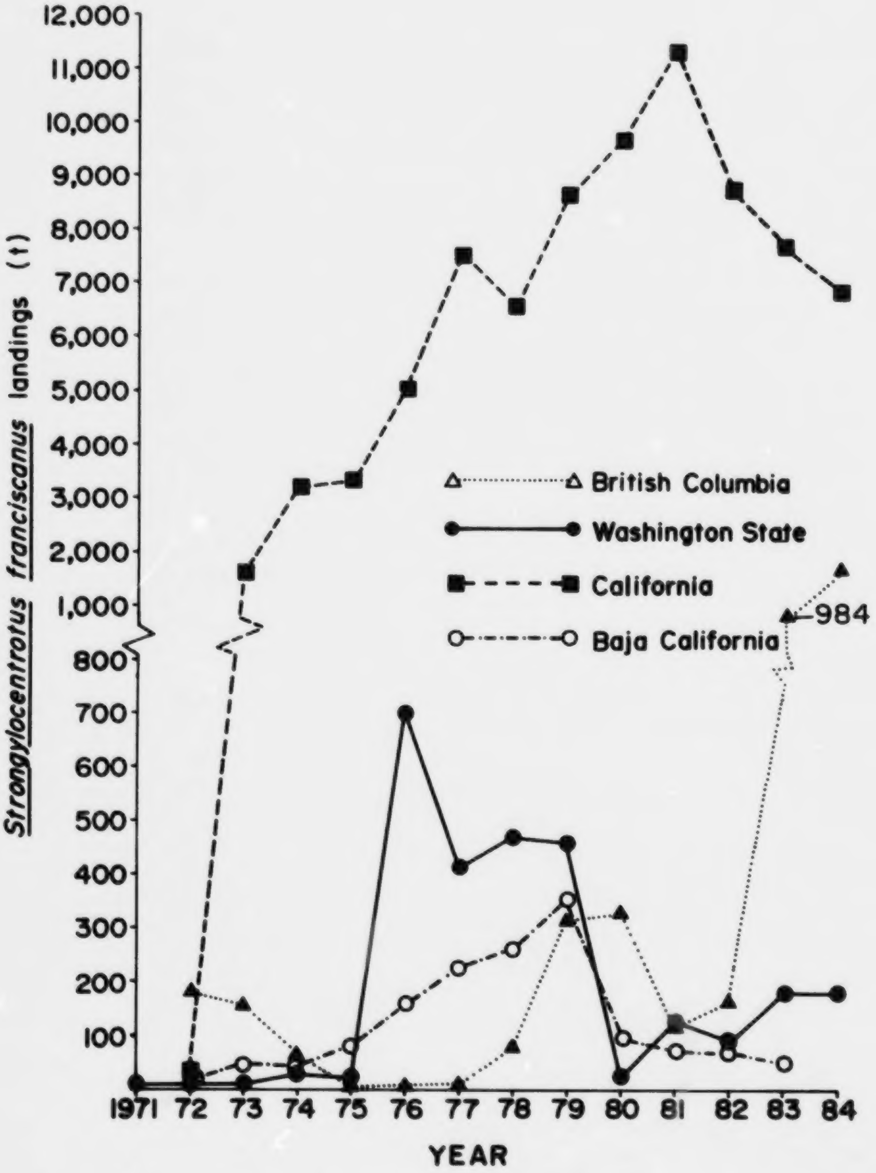

FIG. 2. Landings of *Strongylocentrotus franciscanus* along the Pacific coast of North America. Data from various regional management agencies and M. J. Tegner.

1981, U.S. landings accounted for 22% of the reported world sea urchin catch (Sloan 1985).

Purple urchins, *Strongylocentrotus purpuratus*, and green urchins, *S. droebachiensis*, both of which yield edible roe (Kramer and Nordin 1978, 1979), are little utilized in the northeast Pacific. Handling constraints due to their smaller size render these species less economical to process (Bernard 1977; Breen 1980; Tegner and Dayton 1981). Purple urchins are, however, a valuable resource for developmental biology research and teaching in California (Tegner and Dayton 1981).

The small Mexican (Baja California) fishery has grown steadily to landings of 352 t in 1979 but has since declined (Fig. 2; M. J. Tegner, pers. comm.). Whether this recent decrease is due to abundance decline or marketing problems is unknown.

Southern California *S. franciscanus* landings dominate the northeast Pacific fishery (Fig. 2). This fishery is considered fully exploited with most landings reported from traditionally exploited areas (Hardy et al. 1982), and is now in decline (Pleschner 1985). A major constraint on expansion of harvesting to central and northern California is sufficiently rapid transport of fresh roe from distant grounds to the Japanese market and limited good weather conditions (D. O. Parker, pers. comm.).

No landings have been recorded in Oregon (D. Demory and I. Robinson, pers. comm.).

The Washington State fishery is rebuilding slowly from a decline after the relatively high landings period of 1976–79 (Fig. 2). The instability of the fishery was caused by depletion of the most accessible shallow-water stocks. This initiated more expensive harvesting of deeper-water stocks, which yielded less marketable, lower quality roe (B. Pease, pers. comm.).

Landings in British Columbia were low until processing and marketing improvements occurred in 1979 (Fig. 2; R. M. Harbo, pers. comm.). After a decrease in production during 1981 and 1982, landings increased strongly to 1768 t in 1984. Divers are being attracted from other diver fisheries such as abalone and geoduck clam (R. M. Harbo pers. comm.). Unfished urchin stocks exist along the less accessible northern British Columbia coast (Breen 1980), but exploitation of northern urchins will require development of regional processing facilities which are accessible by air transport (R. M. Harbo, pers. comm.).

Sea urchins are considered an underutilized resource of potential commercial value in Alaska (Wilson and Gorham 1982). Minor exploratory harvesting has taken place in the Ketchikan area (55°00'N) in southeast Alaska for both red and green urchins since late 1984 (T. Koeneman, pers. comm.). Twenty-two short-term (2-week) harvesting permits have been issued which allow managers to monitor landings and map harvestable beds as exploration occurs. Mixed landings (≈ 27.7 t) of red and green urchins have been reported (T. Koeneman, pers. comm.). Further north in the Cook Inlet area (59°30'N) of south central Alaska, exploratory fishing for green urchins only is underway (J. N. Paul and A. J. Paul, pers. comm.). Between September and November, roe quality is prime and comprises 21–25% of the whole live weight of individuals; maximum size can be up to 70 mm test diameter (Paul and Paul 1984). The major constraint to development of a fishery is transport of fresh roe to the Tokyo market.

Management

North American fishery regulations governing *S. franciscanus* exploitation in 1983 are summarized in Table 3. No management data were available on the Mexican fishery which is apparently run by local cooperatives (M. J. Tegner, pers. comm.). The southern California fishery is relatively unmanaged, with market activity controlling effort. Recent declines in stocks have stimulated desire in both management and industry sectors for more control of harvesting through regu-

TABLE 3. *Strongylocentrotus franciscanus* fishery regulations along the Pacific coast of North America, 1983.

	Commercial fishery regulations						Recreational fishery regulations
	Closures						
Area	Area	Season	Landings quota	Size limit[a]	Mandatory log book	Licence restrictions (number of vessels licensed)	Daily bag limit
British Columbia	Yes[b]	June – August	Yes[c]	≥100	Yes	diving only: 'Z' licence[d] (64)	Yes[e]
Washington State	Yes[f]	Yes[f]	No	Yes[g]	Yes	diving only: 'dip bag' licence[h] (116)	18
California	No	No	No	No	No	diving only: 'invertebrate' permit[i] (250)	No

[a] Test diameter (mm).

[b] Vancouver area and SE Strait of Georgia closed because of proximity to the large urban area.

[c] SE and S of Vancouver Island, i.e. SW Strait of Georgia and Gulf Islands annual quota of 136 t.

[d] A species-specific tab licence; 29 of the 64 licensed vessels reported landings in 1983.

[e] A bag limit of 12 (any sea urchin species) in effect in National Parks.

[f] Outer coast no closure; outer Juan de Fuca Strait open October–April in even years only; inner Juan de Fuca Strait open October–April in odd years only; San Juan Islands are open September only each year.

[g] San Juan Islands area (sheltered) 114–140 mm (4.5–5.5"); outer coast and Juan de Fuca Strait (exposed) 95–140 mm (3.75–5.5").

[h] Within this diving- and net-licence are herring, smelt, squid, sea cucumber, and sea urchin fisheries. Sea urchin boats receive a special number within the licence system. Six vessels landed sea urchins in 1983.

[i] A diving licence for registered fishermen to harvest sea urchins (or sea cucumbers) within 305 m (1000 ft) from shore.

lation (Pleschner 1985). Commercial urchin fishing in California was originally seen as a boon by the fisheries community and urchins are still being eradicated in some areas as pests of harvestable kelp (*Macrocystis pyrifera*) resources (Kato 1972; McDaniel 1975; North 1976; Nathensen 1980; Wilson and North 1983; Pleschner 1985). Recruitment of *S. franciscanus* in southern California appears annual and "substantial" in some areas (>30% of the population per year; (Tegner and Dayton 1981; Ebert 1983)). Managers estimate that fished beds need 4-5 years to regenerate a harvestable biomass although field verification is still needed (D. O. Parker, pers. comm.). Recent landings have declined due to the El Nino event, massive storms, the high $U.S. value relative to other currencies and perhaps overfishing (Dayton and Tegner 1984a; Pleschner 1985; M. J. Tegner, pers. comm.).

The shelter for recruits provided by the spine canopy of larger adults represents a significant nursery habitat resource warranting management concern in California (Tegner and Dayton 1977). Young *S. franciscanus* recruit and grow in safety (to 30-40 mm test diameter) under conspecific adults (Tegner and Dayton 1977). Sea urchins 50-80 mm are not protected and are thus very vulnerable to predation before reaching a partial size refuge at approximately 90 mm (Tegner and Dayton 1981; Tegner and Levin 1983). Harvesters should ensure that some large urchins remain as recruitment shelters for juveniles. Furthermore, large *S. franciscanus* may also shelter small abalone (*H. rufescens*) under their spine canopies and urchin grazing may promote crustose red algae areas which are prime abalone recruitment sites (Dayton and Tegner 1984b; Morse and Morse 1984). In southern Japan, commercial urchins *Anthocidaris crasspina* enhanced the survival rate of introduced juvenile *Haliotis discus discus* from 0-4% to 23-28% by providing spine canopy shelter (Kojima 1981).

In Washington State, a suite of size limits, area, seasonal, and annual closures control fishing effort (Table 3). Overfishing did occur in the late 1970s, but is now under control (B. Pease, pers. comm.). There is lobbying by processors to allow harvesting of smaller urchins as their roe is more acceptable in size and quality to Japanese buyers. Management of the fishery is in transition. Detailed data collection began in 1975 (Anon. 1977). Verification of alleged low recruitment in some areas and improved estimates of harvested-area recovery rates are needed for better long-term stock status prediction (Jones 1977; L. Goodwin, pers. comm.).

Management of the British Columbia sea urchin fishery is also evolving but, unlike southern California and Washington State, the largest stocks remain unfished (P. A. Breen and R. M. Harbo, pers. comm.). As with sea cucumbers, management has tended to be preemptive to control harvesting in the face of incomplete biological information (Table 3). Bernard (1977) suggested two main areas of management concern for British Columbia urchin resources: significance of gregarious urchin behavior to reproduction, and recolonization of harvested areas.

The October to April fishery is closed at other times of the year to prevent harvest of low quality (post-spawned) urchins. Seasonal closures can, however, be lifted according to site-specific conditions in a particular year (R. M. Harbo, pers. comm.).

British Columbia *S. franciscanus* first reproduce at 50 mm test diameter (Bernard and Miller 1973a, b) and the legal size of 100 mm may be reached in 4 to 5 years (Breen and Adkins 1978). All adults ≥ 95 mm test diameter are potentially 'parental' as they shelter juveniles, similar to California urchins (Breen 1984; Breen et al. 1985). The present size limit permits harvesting of most of the 'parental' stock but prevents access by the industry to the best quality roe. As in Washington State, processors are lobbying management to decrease the size limit to permit smaller (≈ 75 mm), more valuable roe in the market. Furthermore, roe of the largest urchins (>125 mm) is generally of inferior quality which further increases desirability of smaller size classes (R. M. Harbo, pers. comm.). Decreasing the British Columbia size limit to 75 mm would render approximately 23% more of the population vulnerable to fishing (Breen 1984) and remove protection of all 'parental' adults. Despite annual spawning, recruitment is low overall (Bernard 1977; Breen and Adkins 1978; Breen 1980; Admins et al. 1981), leading to a poor recovery rate of harvested populations (Breen and Adkins 1978). Low recruitment (≈ 5.5% of the population per year) in the southeastern Vancouver Island and adjacent islands areas (Adkins et al. 1981) has led to low regional landing quotas (Table 3).

Breen (1980) has reviewed management options for harvesting northern urchins characterized by low recruitment and growth rates. Harvesting in a sustainable fishery would have to be low for such a population (Breen and Adkins 1978). Managers could focus and control effort by landing quotas or rotate openings on annual or longer terms. They could also vary harvestable sizes to manipulate the proportion of the population vulnerable to fishing, although Breen (1984) suggests effort control should supplement size limits.

Breen and Adkins (1978) stress that fishery costs and product handling could confound theoretical management systems because of the economic necessity of intense harvesting (unrestricted effort) in small areas. Intense harvesting, i.e. 'pulse' fishing, in rotating areas is a possibility. Urchin populations would become locally depressed but the distribution and productivity of kelp forests in these areas could be enhanced (Breen 1980). There exists a 'trade-off' between overregulating a small, embryonic fishery requiring encouragement on one hand, and local sea urchin-kelp forest ecosystem concerns on the other.

Urchins, Kelp Forest Community Structure and Multispecies Management

Urchins are enormously important as grazers of algae in many temperate rocky subtidal communities throughout the world (Lawrence 1975; Lawrence and Sammarco 1982). The production of roe by urchins is dependent upon availability of algae food resources (Fuji 1967) and, therefore, understanding the ecology of urchin-algae interactions is important to urchin fisheries management (Kawamura 1973).

An extensive literature exists on the role of certain abiotic (severe storms; sea water temperatures) and biotic (urchin grazing) factors on kelp forest community structure in central and southern California (Cowen et al. 1982; Breitburg 1984; Dayton 1984; Dayton and Tegner 1984a, b; Dayton et al. 1984; Dean et al. 1984; Ebeling et al. 1985; Harrold and Reed 1985). Community states vary between encrusting algae–urchin barrens, various algae canopy guilds, and tall perennial canopies of *Macrocystis*. The frequency of storms removing tall plants, temperature and nutrient conditions favoring algae recruitment and growth, and availability of drift algae food to *S. franciscanus* are key community-structuring situations. When intact, the kelp forest canopy generates abundant drift algae and urchins are cryptic, sedentary, and feed on entrapped drift algae. In this community state, urchins will be in good condition for harvesting as their roe yield will be high. When storms reduce the forest canopy, hungry urchins (with lower gonadal indices) emerge from shelter to graze attached plants, which further decreases kelp abundance and can lead to relatively barren substrates. Eventual recruitment, survival, and growth of canopy-forming algae species under appropriate cool temperatures and high nutrient conditions, may reverse this process and reestablish kelp abundance until the next severe storm event. With knowledge of these processes, fisheries managers can assess the state of local kelp forests and predict urchin roe production.

Management of urchins can be complicated by the necessity of considering other harvestable kelp-associated resources. For example, destructive grazing by *S. droebachiensis* along the east coast of Nova Scotia has stimulated intense ecological interest and much debate concerning effects on other inshore fisheries resources, notably lobster (Mann 1982; Pringle et al. 1982; Scheibling 1984; Miller 1985). Tegner (1980) has suggested the need for a multispecies approach to managing southern California kelp forest resources for urchin, lobster, abalone, various finfish, and kelp. For example, harvesting of two urchin predators, the spiny lobster *Panulirus interruptus* and the sheephead wrasse *Semicossyphus pulcher*, has released predation pressure on *S. franciscanus* (Tegner and Dayton 1981; Cowen 1983; Tegner and Levin 1983). Competition for similar food and microhabitats, which may have occurred in the past between red abalone, *Haliotis rufescens* and *S. franciscanus* (Tegner and Levin 1982), has probably been decreased by abalone fishing. Tegner and Levin (1983) correlated apparent urchin population increases with substantial decreases in lobster and abalone landings.

Multispecies interaction at higher latitudes may decrease in importance. North of California to Alaska, there are fewer significant predators of *S. franciscanus*. Duggins (1983) suggests that, with the exception of pockets of sea otters, the sea star *Pycnopodia helianthoides* is the only noteworthy urchin predator. *P. helianthoides* clears patches of urchins, thus aiding algal succession, production and species richness (Dayton 1975; Duggins 1983). In British Columbia, *S. franciscanus* is capable of controlling the lower depth limit of kelp forests (Pace 1981). Localized destructive overgrazing has also been recorded (Breen and Adkins 1979), but large-scale urchin population explosions, as reported from California, have not been observed.

The near extinction of the sea otter, *Enhydra lutris*, through hunting may have initiated marked ecological changes in nearshore communities when its prey populations of urchins, abalones and other invertebrates were released from predator pressure (Simenstad et al. 1978; Duggins 1980). Duggins (1983) mentions that where sea otters have become reestablished, such as in Pacific Grove, northern California (Lowrey and Pearse 1973) and off the northwest Vancouver Island coast (Breen et al. 1982), their predation pressure on urchins has led to increases in local kelp forests. These are only localized situations, however, as most of the coast is still unpopulated by sea otters. Duggins (1980) has stressed that the continued spread of sea otters may have important implications for nearshore fishery resource management in the future.

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Cephalopod Fisheries of the North Pacific and Their Management

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JEFFERTS, K. 1986. Cephalopod fisheries of the North Pacific and their management, p. 34–56. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

Cephalopod fisheries in the North Pacific are dominated by the Japanese, with some American and Mexican harvesting off the Californias. Historically, the Japanese cephalopod fishery concentrated on *Todarodes pacificus*, with minor landings of neritic squids, cuttlefishes, and octopuses. Recent declines in landings of *Todarodes pacificus* have prompted expansion of Japanese fishery efforts into other regions. In the North Pacific a number of other species are now targeted. Cephalopods are also important in fisheries of most of southeast Asia. Fishing methods and landings are described.

Management of the Japanese cephalopod fishery is centred on problems of overcapitalization and maximization of employment, rather than conservation of the resource. Life cycle and general ecology of *Todarodes pacificus* and steps necessary for effective management of this resource are fairly well understood, but difficult to implement for socio-political reasons. Considerably less information on life history and ecological relations is available for effective management of other species. The need for such data appears urgent, as some of these other fisheries appear to be at or above the level of harvest required for optimum yield, particularly the *Octopus vulgaris* resource in the Seto Inland Sea and the *Ommastrephes bartrami* fishery. Management of the offshore fisheries has also been concerned with preventing conflict with the high seas salmon fishery and minimizing competition with the squid jigging fishery.

Several species of cephalopods represent potential fisheries in the northeastern Pacific. The only significant existing cephalopod fisheries in the northeastern Pacific are those for *Loligo opalescens* in California and *Dosidicus gigas* in the Gulf of California. Fishery methods for these and other species are considered, both in traditional and non-traditional regions. Management of the *Loligo opalescens* fishery has become an issue only recently, with most requirements aimed at avoiding disturbance of demersal eggs. The recent El Niño–Southern Oscillation event (ENSO) had a major influence on this fishery, with unknown long-term effects. Adequate management of this species will require at least stock size estimation and information on recruitment relations. Little is known of the life history and recruitment processes of other potentially exploitable species in the northeastern Pacific.

Dans le Pacifique Nord, la pêche aux céphalopodes est dominée par les Japonais, même si une partie des récoltes est pratiquée par les Américains et les Mexicains au large des deux Californies. Sur le plan historique, la pêche japonaise aux céphalopodes s'est concentrée sur *Todarodes pacificus*, avec de petits débarquements d'encornets néritiques, de seiches et de poulpes. Les récents déclins enregistrés dans les débarquements de *Todarodes pacificus* ont accéléré l'expansion des efforts de pêche japonais dans d'autres régions. Dans le Pacifique Nord, de nombreuses autres espèces sont maintenant visées. Les céphalopodes sont également importants dans les pêches de la plus grande partie du Sud-Est asiatique. L'auteur décrit ici les méthodes de pêche et les débarquements.

La gestion de la pêche japonaise aux céphalopodes est centrée sur les problèmes de surcapitalisation et de maximisation de l'emploi, plutôt que sur la conservation de la ressource. Le cycle biologique et l'écologie générale de *Todarodes pacificus* ainsi que les étapes nécessaires pour une saine gestion de cette ressource sont relativement bien compris, mais difficiles à mettre en œuvre pour des raisons socio-politiques. Il existe beaucoup moins d'informations concernant les antécédents biologiques et les relations écologiques pour une gestion efficace des autres espèces. Le besoin de telles données semble urgent, puisque certaines de ces autres pêches semblent se situer au niveau de récolte requis pour un rendement optimal ou au-dessus de ce niveau, particulièrement en ce qui concerne la ressource en *Octopus vulgaris* dans la Mer intérieure du Japon et la pêcherie d'*Ommastrephes bartrami*. La gestion de la pêche au large des côtes porte aussi sur la prévention de conflits avec la pêche au saumon en haute mer et la minimisation de la concurrence avec la pêche de l'encornet à la turlutte.

Plusieurs espèces de céphalopodes représentent des pêcheries potentielles dans le Nord-Est du Pacifique. La seule pêcherie de Céphalopodes importante qui existe actuellement dans le nord-est du Pacifique est celle de *Loligo opalescens* en Californie et de *Dosidicus gigas* dans le golfe de Californie. Des méthodes sont envisagées pour ces pêcheries ainsi que pour d'autres espèces, tant dans les régions traditionnelles que dans les régions non traditionnelles. Il n'y a pas tellement longtemps depuis que l'on a commencé à s'intéresser à la gestion de la pêche aux *Loligo opalescens* et la plupart des exigences visent à éviter le dérangement des œufs démersaux. L'événement récent connu sous le nom d'El Niño–Southern Oscillation (ENSO) a exercé une influence considérable sur cette pêche et on en ignore encore les effets à long terme. La bonne gestion de cette espèce nécessitera au moins une estimation de la taille des stocks et des informations concernant les relations de recrutement. On ne sait pas encore grand chose au sujet des antécédents biologiques et des processus de recrutement concernant les autres espèces potentiellement exploitables dans le Nord-Est du Pacifique.

Introduction

Cephalopod fisheries represent just over 2% of landings of total world fisheries (1982 total landings, all fisheries, 76 772 800 t — FAO 1984); landings have averaged about 1.5 million t during the last 4 yr for which statistics are available (Table 1). About 60% of this was harvested from the North Pacific (FAO statistical areas 61, 71 (not including Australia), 67, 77 (see FAO 1984 for limits of these areas)) in 1982, primarily by Japan, although significant landings were also made by vessels of Korean, Thai, Chinese, Soviet, and Philippine registry (Table 2).

TABLE 1. Landings (t) of Cephalopods in the North Pacific (FAO statistical areas 61, 67, 71, 77), by species and producing nation, for 1979 through 1982 (FAO 1984).

	1979	1980	1981	1982
Squid				
Todarodes pacificus				
Japan	212 846	330 464	196 830	181 721
Korea Rep.	26 132	48 490	62 403	66 202
TOTAL	238 978	378 954	259 233	247 923
Loligo spp.				
Thailand	37 293	36 203	43 778	42 740
Philippines	25 495	27 011	27 980	20 989
Indonesia	11 921	10 227	7 798	10 421
Others	469	521	588	766
TOTAL	75 178	73 962	80 144	74 916
Unidentified — mostly ommastrephids and loliginids				
Japan	207 097	238 928	225 212	268 413
China	90 127	79 518	28 131	49 931
USSR	30 752	26 422	22 620	26 930
USA	16 011	11 442	21 650	16 323
Korea Rep.	631	6 418	1 526	10 773
Malaysia	12 014	8 983	12 103	9 634
Hong Kong	6 139	4 104	5 407	5 164
Others	30 041	26 490	31 288	32 498
TOTAL	392 812	402 305	347 937	419 666
Cuttlefish				
Sepia spp., *Sepiola* spp.				
Korea Rep.	55 663	38 922	38 153	31 874
Thailand	26 293	23 475	23 582	22 916
Viet Nam	11 100	11 600	12 100	12 600
Japan	14 148	10 409	7 072	7 572
Malaysia	4 728	3 747	4 603	2 284
Indonesia	1 783	1 932	862	2 161
Hong Kong	1 711	1 814	1 601	1 414
Philippines	2 368	3 129	3 238	1 331
Others	16 406	19 307	27 757	28 742
TOTAL	134 200	114 335	118 968	110 894
World Catch	196 857	173 475	168 628	170 793
Octopuses				
Octopodidae				
Japan	42 375	46 108	45 399	42 584
Korea Rep.	7 185	8 374	7 732	8 803
Thailand	7 234	5 738	5 347	5 274
Philippines	1 390	1 592	1 296	1 579
Others	1 184	1 323	1 287	1 663
TOTAL	59 368	63 145	61 061	59 804
World Catch	123 814	153 149	181 159	188 756
All Cephalopods				
World Catch	1 512 825	1 529 170	1 353 982	1 567 179

The Class Cephalopoda includes the familiar squid, cuttlefishes, and octopods, as well as the chambered nautilus and vampire squids. Nautiluses are not discussed in this review. They are limited to the Indo-West Pacific, and are important in artisanal fisheries, for food and for shell products and live display (Roper et al. 1984). Cephalopods are found in all oceans from the poles to the tropics, but generally only where salinity exceeds 30‰ (Laevastu and Ficus 1978; Brakoniecki 1980). They range in total length from a few centimetres to nearly 20 m, and in weight from a few grams to about 1 t. Most cephalopods have short lifespans (commercial squids are primarily annual species) and are generally thought to die shortly after reproducing (Boyle 1983; Mangold 1983a). All cephalopods are predatory carnivores, and most are high on the food chain. Many are important in the diets of salmonids, other oceanic fishes, marine mammals, and seabirds (Okutani and Nemoto 1964; Manzer 1968; Okutani et al. 1976; Fiscus 1978, 1980, 1982; Morejohn et al. 1978; Clarke and MacLeod 1980; Clarke 1980, 1983; Amaratunga 1983; Antonelis and Perez 1984).

The squid (Order Teuthoidea) comprise 300–350 species in 25 families (Lipinski 1973; Okutani 1977; Roger et al. 1984). Commercially important squids are nearly all in the families Ommastrephidae and Loliginidae, which together comprise two-thirds of the world cephalopod catch (Table 1). *Todarodes pacificus* is the most important species, producing about one-third of

TABLE 2. Cephalopod landings (t) from the North Pacific (FAO statistical areas 61, 67, 71, 77) by nation, for 1979 through 1982 (FAO 1984). Others includes all landings not identified to nation.

	1979	1980	1981	1982
Japan	476 466	625 909	474 513	500 191
Korea Rep.	89 611	102 204	109 814	117 652
Thailand	70 820	68 052	72 707	70 930
China	90 127	79 518	28 131	49 931
USSR	30 830	26 444	22 723	26 930
Philippines	29 253	31 732	32 514	23 899
USA	16 031	11 442	21 650	16 323
Indonesia	13 741	12 212	8 703	12 686
Viet Nam	11 100	11 600	12 100	12 600
Malaysia	16 742	12 730	16 706	12 332
Hong Kong	7 850	5 918	7 008	6 578
Singapore	642	585	708	855
Australia	120	219	234	257
Mexico	105	65	356	244
Colombia	20	12	22	106
Cook Islands	60	60	60	60
Canada	35	51	29	12
Fiji	4	9	13	12
Costa Rica	3	2	2	8
New Caledonia	2	7	7	7
Poland	35	12	118	—
Pacific Trust Territories	9	0	0	0
Others	46 930	46 554	59 225	61 590

Japanese squid landings in the North Pacific. Stocks of loliginid squids are not large in the western Pacific, but do support significant local fisheries.

About 7500 t of cuttlefish were taken around Japan in 1982. Large quantities were also taken in the northwestern Pacific by Thailand, Korea, and Viet Nam; no other significant stocks are present in the North Pacific (Okutani 1977; FAO 1984). Although there are some 100 species of cuttlefish in two primary families (Hotta 1976), very few are of commercial importance, and none is found in the eastern Pacific.

World catches of octopuses totaled 206 608 t in 1982, including 19 species of primary commercial importance (Voss 1973; Briantais 1974; Hotta 1976; Sakamoto 1976; FAO 1984). The North Pacific yielded nearly 60 000 t of octopuses in 1982, with Japan landing 70% (Table 1). Only a small fishery exists in the eastern Pacific.

Japanese Fisheries

Japan leads the world in cephalopod consumption; domestic demand for cephalopods exceeds 500 000 t per year and may reach 600 000 t (Kawakami 1977; Tomiyama and Hibiya 1978; Court 1982). Cephalopods have a long history of exploitation in the Japanese islands, from cuttlebones in prehistoric shell middens, to a major dried-item export trade in 1661–1741, and an export trade with China after 1845 (Oako and Murata 1983). The 19th century Chinese market was also supplied by California fisheries.

In the last 15–20 years Japan's landings have ranged from 450 000 to 750 000 t (Court 1982), approximately 32% of the total world cephalopod catch in 1982 (Table 1). Japan imports a significant portion of the rest of the world catch; in 1978 the import quota was 100 000 t (Court 1980). Eight species of squid and cuttlefish, both domestic and imported, form the bulk of the market. Five are taken in the North Pacific: *Todarodes pacificus, Loligo edulis, Ommastrephes bartrami, Sepia officinalis, S. esculenta* (Doumenge 1980; Hotta 1982).

The Japanese fishery has been historically characterized by a large fleet of small boats operating close to shore. In recent years more than 30 000 vessels ranging in size from 1 to 500 t have been employed in different cephalopod fisheries. Jigging vessels predominate, with large and small trawlers, beach seiners, and blanket netters of lesser importance; a few of the larger vessels now employ drift gillnets (Ogura 1983). Squid fishing is conducted primarily with lights and jigs, while cuttlefish and octopuses are usually caught in stationary nets and traps, on hook and line, or with bottom trawls. More than 150 species of cephalopods are present around Japan but *Todarodes pacificus* has been the predominant species taken. In the last few years, *Ommastrephes bartrami* has become important in the offshore jig and gillnet fishery (Fig. 1). Landings of these two species exceeded 464 000 t in 1980 (Court 1982). Cuttlefish and octopus retain a minor importance, with landings of about 20 000 t and 50 000–60 000 t, respectively (Osako and Murata 1983).

The cephalopod fisheries in Japan seem to be regulated by supply and demand, although management for MSY might increase supply. As in many productive fisheries, exploitation has outpaced research, making management difficult. Recent efforts have improved the understanding of population dynamics, and predictive models are beginning to be developed. Other problems in the Japanese squid fishery are high fuel costs, excessive competition, and great price and supply fluctuations (Court 1980, 1982).

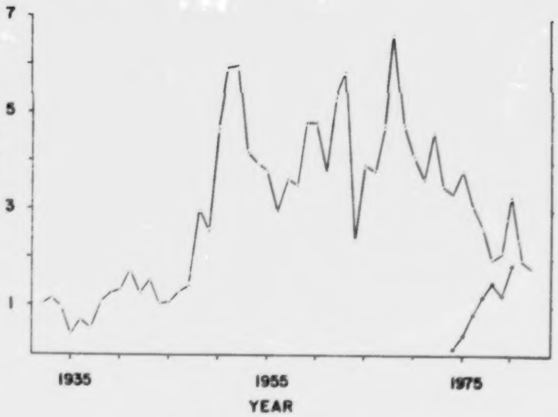

FIG. 1. Landings (t) of *Todarodes pacificus* (dots) and *Ommastrephes bartrami* (open circles). Data from Murata (1983b), Murata et al. (1983), Osako and Murata (1983), and FAO 1984.

The coastal cephalopod fisheries are managed by Sea Area Fisheries Adjustment Committees, which are limited in geographic jurisdiction and political influence. Their prime directive is to arbitrate disputes, thus they manage the conduct of fisheries rather than fisheries resources (Keen 1979, cited in Court 1980). This management by multiple entities has encouraged disparate policies and discouraged resource management (cf. "the tragedy of the commons"). Management efforts of the national government have emphasized continued employment and fishery development rather than conservation (Court 1980). The fishery is essentially free-entry; although licensing has been recently imposed, licenses are freely transferrable, and little effort has been made to reduce their numbers, thus ensuring continued excessive competition. Specific management directives for individual fisheries are discussed in species accounts.

Fisheries in the Eastern Pacific

Although more than 60 species of cephalopods are present in the eastern and northeastern Pacific (Berry 1912; Young 1972; Jefferts 1983), only a few are subject to any directed fishery (Rathjen 1983). *Loligo opalescens* and *Dosidicus gigas* are the most important commercially harvested species; annual catches of each are 10–20 thousand t. A number of species are present in some abundance in the Subarctic eastern Pacific (Table 3), but most are not commercially desirable due to ammoniacal tissues, or lack of market or processing technology. The lack of appropriate harvesting methods for non-schooling forms is also a hindrance.

Fisheries of other nations around the North Pacific are small compared to those of Japan, and are discussed

TABLE 3. Species of cephalopods abundant in the northeastern Subarctic Pacific. Third column — gear used for species commercially harvested or reason for non-harvest, if known. (after Okutani 1977; Bernard 1980).

Species	Family	Gear/NH
Rossis pacifica	Sepiolidae	small size
Onychoteuthis borealijaponica	Onychoteuthidae	jig/incidental
Moroteuthis robusta	Onychoteuthidae	ammoniacal?
Symplectoteuthis luminosa	Onychoteuthidae	not harvested
Gonatopsis borealis	Gonatidae	incidental
Gonatus spp.	Gonatide	small/ammoniacal
Berryteuthis magister	Gonatidae	bottom trawl
Berryteuthis anonychus	Gonatidae	not harvested
Ommastrephes bartramii	Ommastrephidae	gillnet
Histioteuthis dofleini	Histioteuthidae	ammoniacal

under individual species accounts. A summary of cephalopod fisheries in the Indo-West Pacific is given in Chikuni (1983).

Species Accounts

Todarodes pacificus

Todarodes pacificus is an ommastrephid squid endemic to the northwestern Pacific (Table 4), although it may occasionally occur in the northeastern Pacific. Three subpopulations are present, which breed in different seasons: winter, summer, and autumn (Fig. 2). Each subpopulation is represented by a stock in the Japan Sea and one in the Pacific east of Japan, and each has a characteristic north–south migration pattern. The winter subpopulation, which occurs from the East China Sea to about 45°N in the middle Kuriles and off Sakhalin, is the primary target of the traditional fishery on the Pacific coast of northern Honshu and Hokkaido (Fig. 2). The autumn stock supports the bulk of the offshore Japan Sea fishery, harvested from October to December, with a peak in November. Together, the winter and autumn subpopulations account for about 90% of all *Todarodes* landings. The summer subpopulation and the Pacific component of the autumn stock are small, and support only local fisheries off the Pacific coast.

The life cycle of this species is approximately annual. *Todarodes pacificus* lays approximately 320 000 to 470 000 demersal eggs, which may float secondarily (Okutani 1983; Amaratunga 1983). Hatching requires 4–5 d at 14–21°C (Hamabe 1962) and about 11 d at 10–13°C (Hayashi 1960). Hatchlings, called rhynchoteuthion larvae, are 0.75–1.00 mm DML (dorsal mantle length) and appear primarily in January and February (winter population) between the Korean peninsula and Kyushu. The youngest stages occur only in waters above 18°C and 19.2‰, and are most abundant at 20–22°C, 19.25–19.35‰ (Watanabe 1965; Shojima 1972). Later stages may occur in water as cold as 10°C (Okutani 1968). They are transported northeast in the Kuroshio Current, reaching their northern limit (52°N in the Sea of Japan, 49°N in the Pacific) in August, having grown to about 200 mm DML. Maturing individuals (males mature first, inseminating immature and maturing females; see Clarke, 1966 for description of mating behaviour) begin a southward migration in the Oyashio in September through November. Tagging studies have shown migration rates as high as 32 km·d^{-1} (Machinaka 1959); Araya et al. (1958) postulated a rate up to 75–95 km·d^{-1}. Mature individuals (24–33 cm DML) spawn southwest of Kyushu and south of Korea between January and March or April.

Similar migrations occur in the other two subpopulations, with variations in timing. Young of the autumn population appear between September and November, spreading north as far as 45–46°N in summer. This stock matures at a size of 24–33 cm DML, beginning its southward migration by September to spawn southwest of Kyushu and south of Korea from September to December (Okutani 1983; Osako and Murata 1983).

The summer stock spawns from May to August or September in limited areas on both coasts of central Honshu (Fig. 2). Maturity occurs at 23–27 cm DML (Okutani 1983; Osako and Murata 1983).

Each stock has a tendency to aggregate in large schools for feeding and for mating. This species migrates vertically between 150–200 m in the daytime, and the upper 50 m at night (Hamabe 1964). Feeding appears to be heaviest near the bottom (Hamabe and Shimizu 1966), although Okiyama (1965) noted heavy feeding at the surface from 1800 to 2000 h. Feeding aggregations are most likely to be found in frontal areas, small gyres, and large scale current rips where food is also likely to be concentrated (Suzuki 1963; Watanabe 1965; Murakami 1976a). Prey includes crustaceans

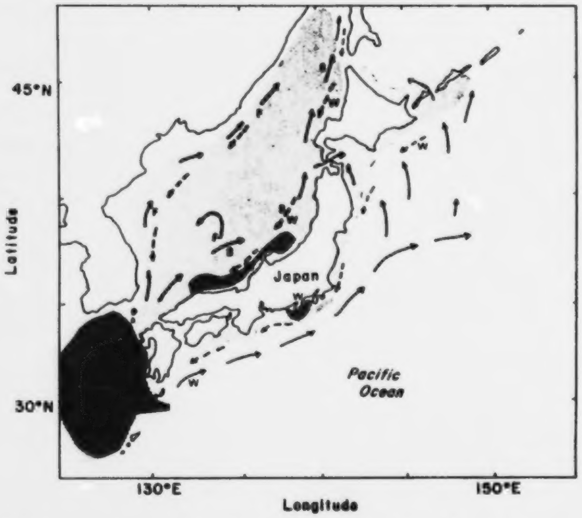

FIG. 2. Western Pacific distribution of *Todarodes pacificus*: fishing grounds (light hatching), spawning grounds (vertical hatching), and migration routes (arrows) for winter (W), summer (S), and fall (F) populations. Data from Okutani (1983) and Osako and Murata (1983).

TABLE 4. Cephalopods of commercial importance in the North Pacific. Key: Niche, BP, bathypelagic; CRF; coral reefs; D, demersal/benthic; EP, epipelagic; MB, mesobenthic; MP, mesopelagic; N, neritic; NB, nektobenthic. Season, month(s) of year when spawning occurs. Fished by (or in): Can, Canada; ECS, East China Sea; HK, Hong Kong; Ind, Indonesia; J, Japan; Mal, Malaysia; Philip, Philippines; SCS, South China Sea; Th, Thailand; YS, Yellow Sea. Parentheses indicate incidental catch. Gear, BN, blanket net; BS, beach seine; BT, bottom trawl; CN, cast net; CP, scoop net; DF, bottom drift net; DH, drag hook; DN, dipnet; FN, fixed net; GN, gillnet; H, hook and line; HN, hoop net; J, jig (squid or octopus); L, lure or baited hook; LL, long line; LM, lampara net; LN, lift net or brail; OT, otter trawl; P, octopus pot or box; PN, pound net; PS, purse seine; PSN, push net; S, seine; SN, set net; SP, spear; T, trawl; TL, troll; TN, trap net; TR, trap; U, pump. Comments: OFN, other places where fished. AQC or cultured, has been reared in culture; Potential, may not now be fished, but has potential. References: 1, Katoh 1959; 2, Chikuni 1983; 3, Okutani 1983; 4, Osako and Murata 1983; 5, Flores 1983a,b; 6, Murata 1983a; 7, Roper et al. 1984; 8, Araya 1983; 9, Nesis 1970; 10, Ehrhardt et al. 1983a,b; 11, Juanico 1980; 12, Blake 1982; 13, Okutani and Tung 1978; 14, Clarke 1966; 15, Kubodera et al. 1983; 16, Hamabe 1978; 17, Tung 1976; 18, Okutani 1977; 19, Jefferts 1983; 20, Okutani and Murata 1983; 21, Fiscus and Mercer 1982; 22, Roper and Young 1975; 23, Naito et al. 1977a,b; 24, Okutani 1980; 25, Shimomura and Fukataki 1957; 26, Fields 1965; 27, Kato and Hardwick 1975; 28, Recksiek and Frey 1978; 29, Spratt 1978; 30, Hochberg 1981; 31, Hixon 1983; 32, Street 1982; 33, Recksiek 1978; 34, Fisher 1981; 35, Dong 1981; 36, Choe 1966; 37, Shin 1982; 38, Sasaki 1929; 39, Okutani and Hatanaka 1976; 40, Sanders 1981; 41, Silas et al. 1982; 42, Voss and Williamson 1971; 43, Singley 1983; 44, Mangold 1983b; 45, Wells and Wells 1977; 46, Anon. 1975; 47, Hamabe et al. 1976a,b; 48, Itami 1976; 49, Akimushkin 1963; 50, Green 1973; 51, Pickford 1964; 52, Mottet 1976; 53, Hartwick 1983; 54, Wilson and Gorham 1982b; 55, Sakamoto 1976; 56, Yamashita 1976; 57, Sato and Hatanaka 1983.

Species	Synonyms	FAO name	Japanese name	Other names	Maximum Size	Geographic distribution	Depth Range	Niche	Season	Fished By	Gear	Comments	References
Todarodes pacificus	*Ommastrephes sloani pacificus*	Japanese flying squid	Surume ika		500 mm, 800 g	Hong Kong to Sea of Okhotsk	0-500 m	N EP MP	1-3,10-12	Japan, S Korea	J	Also spans 5-9	1,2,3,4,5
Ommastrephes bartrami		Neon flying squid	Aka ika	Flying squid	0.3-0.5 m, 1-4 kg	Subtropical North Pacific	0-400 m	EP	1-5	Japan, Taiwan	J GN		4,6,7,8
Dosidicus gigas	*D. eschrichti, D. steenstrupi, Ommastrephes giganteus, O. gigas*	Jumbo flying squid	Amerika oosurume	Jumbo squid	1.3-1.5 m, 50 kg	California-Tierra del Fuego	0-100+ m	N EP MP	12-10	Japan, Mexico	J	OFN: Peru, Korea	7,9,10,11,12
Symplectoteuthis oualaniensis		Purpleback flying squid	Tobi ika		350 mm	Sub-tropical Indo-Pacific	0-1000 m	EP BP	summer	Okinawa, Taiwan	J DN	Also fished in Hawaii	2,7,13
Symplectoteuthis luminosa	*Eucleoteuthis luminosa*	Luminous flying squid	Suji ika		200 mm	Transitional waters	0-1300 m	EP BP		(Japan)	J GN	Incidental, no lg schools	7,14,15,16,17
Nototodarus philippinensis	*N. nipponicus, N. sloani philippinensis*	Philippine flying squid	Fuiripinsurume ika		300 mm, 200 g	Japan-Hong Kong-Philippines	275-600 m	NB		Philippines	T S	OFN: Thailand, Mal, Ind	2,7,16
Nototodarus hawaiiensis	*N. sloani hawaiiensis*	Hawaiian flying squid	Hawaisurume ika		150-160 mm	Hawaiian Islands	0-600 m	EP MP		Hawaii	J GN	Significant potential	7,16
Onychoteuthis borealijaponica	*O. banksi* (pars)	Boreal clubhook squid	Tsume ika	Nail squid	370 mm, 1.1 kg	Transitional-subtropical	0-?	EP	winter	(Japan)	J GN	Incidental	4,15,18,19,20
Gonatopsis borealis		Boreopacific gonate squid	Tako ika	Eight-armed squid	480 mm	Subarctic	0-700 m	EP MP		(Japan)	J GN	Incidental	18,19,21
Berryteuthis magister	*Gonatus magister, G. septemdentatus*	Schoolmaster gonate squid	Dosu ika	Red squid	320 mm	Subarctic	200-1000 m	NB	6-10	Japan (USSR)	OT		7,19,22,23
Thysanoteuthis rhombus	*Th. nuchalis*	Diamondback squid	Sode ida		1 m, 20 kg	Warm water cosmopolite	epipelagic	EP		Japan	J L TN		4,7,16,18,24
Watasenia scintillans	*Abraliopsis joubini, A. scintillans*	Sparkling enope squid	Notaru ika		70 mm	Korea-northern Hokkaido	0-600 m	MP BP	3-8?	Japan	SN	Fished only in Toyama Bay	4,14,18,25
Loligo opalescens	*L. stearnsi*	Opalescent inshore squid	Karidoruma yari ika	Market squid	20 mm, 130 g	Alaska-Baja California	0-100? m	N	1-12	USA (Mexico?)	PS LM BT LN T J U BS DN	Spawning season varies with latitude. AQC	26,34
Loligo edulis	*Doryteuthis kensaki*	Swordtip squid	Kensaki ika		400 mm, 600 g	SW Japan to N Australia	30-170 m	N	4-6	Hong Kong, China	J PT FN PS	OFN: Philip, Indonesia	2,7,16,18
Loligo edulis budo	*L. edulis grandipes*	Budo squid	Budo ika		250 mm	SW Sea of Japan		N	6-10?	Japan, China	J L FN PS		2,7,16,18
Loligo japonica		Japanese squid	Jindou ika		120 mm	S Hokkaido to E China Sea	shallow	N	3-7	Japan, China	SN T		2,16,35
Loligo beka	*L. sumatrensis*	Beka squid	Be ika		70 mm	S Honshu to S China		N		Japan, China		Abundant in Inland Sea	7,16
Loligo chinensis	*L. etheridgei, L. formosana*	Mitre squid	Hirakensaki ika		300 mm	S Honshu-S China Sea-Australia	15-170 mm	N	2-5, 8-11	Taiwan, Th, Ind, China, HK, SCS	T PS SN H CN DN	Probably spawns 1-12. OFN: Philippines, Malaysia	2,7,16,35
Loligo duvauceli	*L. indica, L. oshimai*	Indian squid	—		290 mm, 1.5 kg	Taiwan-Indonesia-Africa	30-170 m	N	1-12	Hong Kong, Philip	PS T	OFN: Thailand, Ind, Mal	2,7
Loligo uyii	*L. gotoi, L. tagoi*	Little squid	—		100 mm	S Honshu to Hong Kong	0-50 m	N		S China Sea	T S	OFN: Thailand, Indonesia	2,7
Sepioteuthis lessoniana	*S. arctipinnis, S. brevis, S. guinensis, S. indica*	Bigfin reef squid	Aori ika		360 mm, 1.8 kg	Hawaii-S Honshu-Australia west to Red Sea	0-100 m	N	5-6	SE Asia, Philip	T DN CN CP S H TR GN	OFN: Thailand, Malaysia. Cultured	2,7,16,24,36,37
Doryteuthis bleekeri		Spear squid	Yari ika		400 mm	Southern Japan to Korea	0-100 m	N	2-7	Japan	BN BT SN TN		4,7

Species	Synonyms	FAO name	Japanese name	Other names	Maximum Size	Geographic distribution	Depth Range	Niche	Season	Fished By	Gear	Comments	References
Doryteuthis reesei		—	—			Philippines		N		Philippines	DN T PS		2
Doryteuthis singhalensis		Long barrel squid	—		500 mm, 1 5 kg	Taiwan Thailand, Seychelles	30-120 m	N	summer	Hong Kong SCS	DN T PS	OFN Philip. Ind. Mal	2,7 38,39
Sepia esculenta	*S elliptica*	Golden cuttlefish	Kou ika		180 mm, 600 g	Honshu to S China Sea	10-100 m	D	3-7	China, J, Philip	T PN HN H	OFN HK, Ind? Cultured	2 4 7 16
Sepia lycidas	*S subaculeata*	Kisslip cuttlefish	Makinari ika		380 mm, 5 kg	S Japan Philippines southern China	60-100 m	D	3-5	J, Philip HK	T TR SP SN S J L	OFN ECS YS Th Ind	2 4 7 16
Sepia kobiensis	*S andreanoides*	Kobi cuttlefish	Himekou ika		90 mm	Honshu to S China Sea	0 160 m	D		Japan Thailand	FN T BS	OFN Hong Kong	2,4,7
Sepia pharaonis	*S rouxi, S formosana, S tigris*	Pharaoh cuttlefish	Toratukou ika		360 mm, 4 2 kg	S Japan-Australia Red Sea	30-100 m	D	3-5	YS ECS Philip	LL SP TR T S L	OFN Thailand Indonesia Spawning time varies in the west	2,7 16,40,41
Sepia aculeata	*S indica*	Needle cuttlefish	Aminonkou ika		230 mm 1 3 kg	S Japan to Sri Lanka	0-60 m	D	3-5	HK, YS ECS Th	SN TR S H T	OFN Philip Indonesia	2 16
Sepia latimanus	*S hercules, S mozambica, S rappiana*	Broadclub cuttlefish	Kobushime		500 mm	S Japan to Australia west to Africa, coral reefs	5-50 m	D CRF	1-5-10	Philip, Th Ind	SP J SN T H	Hatching takes 7-8 weeks	2 7 16
Sepia recurvirostra	*S singaporensis*	Curvespine cuttlefish	Asia kou ika		170 mm 400 g	YS SCS Philippine Sea	50-140 m	D		Philip Th Ind	T S	ONF Hong Kong	2 16
Sepia andreana		Andrea cuttlefish	—		120 mm	N Honshu N Philippines	0-50 m	D		China	T SN		7
Sepia longipes		Longarm cuttlefish	—		200 mm	S Japan		D		? Japan		Potential	7
Sepia madokai	*S robsoni*	Madoka's cuttlefish	—		100 mm	S Japan		D		Japan	DF T		7
Sepia tullbergi	*Metasepia tullbergi*	Paintpot cuttlefish	—		70 mm	S Japan to Taiwan	40-100 m	D		Japan, Taiwan	Artisanal?		7
Sepiella japonica	*S heylei*	Japanese spineless cuttlefish	Shiriyake ika		200 mm 800 g	Honshu to Taiwan	0-50 m	D	5-6 2-3	China Japan	T TR H	Spng 5-6 J 2-3 HK AQC	2,7 16 35 36,42
Sepiella inermis	*S affinis, S maindroni, S microcheirus*	Spineless cuttlefish	—		125 mm	S China Sea to Red Sea	0-40 m	D	4 9-10	Andaman Sea	PSN T S	OFN Thailand Indonesia	2 7
Euprymna morsei	*E similis, Inioteuthis morsei*	Mimika bobtail	Mimi ika		40 mm	Hokkaido Malaysia Indonesia	shallow	D			Artisanal		16 cf 43
Euprymna berryi		Double-ear bobtail	—		50 mm	Hokkaido Philip Sri Lanka	0-60 m	D		China Hong Kong	Artisanal	Cultured	7 16
Sepiolina nipponensis	*Stoloteuthis nipponensis*	Japanese bobtail	—		40 mm	S Japan Philippines	0-200 m	D		?J ?Philippines		Potential	7
Rossia pacifica		North Pacific bobtail	Bouzu ika		100 mm	North Pacific rim	100-600 m	D MB		(Japan)	T	Incidental, low value	16 19
Octopus vulgaris		Common octopus	Ma dako		1 3 m 10 kg	Cosmopolitan warm temperate except northeastern Pacific	0-150 m	D	4-5 9-10	Japan	P T H	Primarily Seto Inland Sea	7 44 48
Octopus dofleini	*O dofleini apollyon, O gilbertianus, O hongkongensis* **	North Pacific giant octopus	Mizu dako	Giant octopus	3 m 50 kg	Korea to N California	0-200 m	D	5-6	Japan Can USA	P DH LL H T SP T	Spawning 5-6 in W Pacific	4 18 49 57
Octopus conispadiceus		Chestnut octopus	Yanagi dako		1 5 m 4 kg	Japan Kuriles Sakhalin	100 m +	D	winter	Japan	T BT LL TR		4
Octopus araneoides		—	Ezokumo dako			N Japan	<200 m	D MB		Japan	T P		7 18
Octopus macropus	*O bermudensis, O chromatus, O cuvieri, O longimanus*	White spotted octopus	—		700 mm	E China Sea Australia Mexico Peru, central Pacific Islands	shallow	D		Philippines	TR H SP T L	Artisanal	2 7
Octopus membranaceus	*O tang-siao, O ocellatus*	Webfoot octopus	Ii dako		300 m 500 g	Honshu G. Thailand Australia	0-60 m	D	12-2	Japan China	P TR	Fished throughout SE Asia	2 7
Octopus variabilis		Whiparm octopus	—		700 mm	Japan	0-200 m	D		Japan China			7
Octopus aegina	*O kagoshimensis*	Sandbird octopus	—		300 mm 400 g	Honshu to Java Red Sea	30-120 m	D		Indo-Malaysia	T TR H		7
Octopus dollfusi		Marbled octopus	—		90 mm 200	E S China seas	shallow	D		SCS ECS	T	Incidental	7
Octopus cyaneus	*O horsti, O marmoratus*	Big blue octopus	—	He'e (Hawaii)	1 2 m 4 kg	Hawaii S Japan Australia	shallow	D CRF		Throughout range	TR SP	Artisanal	7
Octopus globosus		Globe octopus	—		250 mm	S Japan Malacca Strait	shallow	D		Japan ?		Potential	7
Cistopus indicus	*C bursarius, Octopus indicus*	Old woman octopus	—		600 mm 2 kg	Taiwan Java G. Thailand	0-50 m	D		Philip HK	TR H	Fished throughout SE Asia	2,7 42

*Also, *S lunulata, S krempfi, S malayana, S mauritania, S neoguinaica, S sieboldi, S sinensis*

**Also, *O punctatus, Polypus dofleini*

(*Parathemisto japonica*, euphausiids, amphipods, copepods, etc.), fish (*Maurolicus muelleri, Engraulis japonica*, myctophids), and squid, including *T. pacificus* (Okutani 1962, 1983; Okiyama 1965; Kasahara and Nasumi 1976; Flores 1983a). Murata (1983a) described size-specific behaviour under night lights. Youngest juveniles remain at the surface once attracted, and larger individuals become progressively more wary. Larger animals may prey on fish attracted to the lights, such as saury, greenling, sardine, and stickleback. No evidence exists for colour discrimination (Flores 1983b).

The autumn subpopulation concentrates in the frontal zone between the warm Tsushima Current and the cold Liman Current (Japan Sea — Flores 1972). Large catches of winter subpopulation squid result from a feeding migration to the region of Kuroshio-Oyashio convergence.

Juvenile *Todarodes* are heavily preyed on by scombroids, especially bluefin and skipjack (Matsuda et al. 1972; Okutani 1983). Mortality is extremely high for the youngest stages. Only 1–5% survive starvation and predation during the first 15 d. Mortality declines rapidly after about 6–8 mm DML, perhaps in concert with onset of vertical migration (Shojima 1972; Okutani and Watanabe 1983). Predators on larger individuals include *Raja, Coryphaena hippurus*, and marine mammals (Sasaki 1920; Wilke and Kenyon 1954; Nemoto 1957; Kojima 1961).

In contrast to the eastern Pacific fishery for *Loligo* (discussed below), *Todarodes* is fished at a wide range of sizes, from juveniles (10–15 cm DML) taken during their northward migration with set nets or seines, to large individuals (20–25 cm DML) taken by jigging in their northern feeding grounds. Few animals are harvested during the southern migration. This species is rarely taken in gillnets (Kubodera et al. 1983).

Since its inception in the mid 1400s, the fishery for *Todarodes* has been almost exclusively a jig fishery, and up to the 1940s was accomplished with small nonmotorized boats of 1–2 t with total catches under 200 000 t·yr^{-1} (Igarashii 1978a,b; Flores 1982) (Fig. 1). Vessel tonnage is computed in Japan at one-half to one-quarter the value assigned by standard classification schemes (Court 1980). In the 1950s, powered vessels of 10–30 t entered the fishery using more jigging lines and battery-powered fishing lights. Even larger boats (50–100 t) with motorized jigging machines, generator-powered fishing lights (up to several hundred kW — Ben-Yami 1976), and blast freezers were built for fishing squid in the 1960s. In the early 1960s catches exceeded 500 000 t·yr^{-1} primarily from the winter subpopulation southeast of Hokkaido. When landings decreased abruptly after 1968, the focus of the fishery shifted to the autumn subpopulation in the central Sea of Japan. In the 1970s, 100–300 t ocean-going vessels were built for this fishery. Overall trend in fleet composition in the last 20 yr may be summarized as: (1) vastly reduced numbers of non-motorized vessels, now only about 100; (2) relatively constant numbers of motorized vessels under 3 t; (3) a 3- to 4-fold increase in vessels of 3 to 20 t; (4) a 3- to 4-fold decrease in vessels of 20–30 t, accompanied by a similar increase in 30–50 t vessels; (5) a 25- to 50-fold increase in 50–200 t vessels; and (6) an increase from none to about 200 vessels of over 200 t (Osako and Murata 1983). Presently more than 40 000 boats land a total of 200 000 to 700 000 t·yr^{-1}. The catch in 1982 was 247 923 t (FAO 1984).

About 95% of the catch is taken by jigging. The general method is to drift with the current or set a sea anchor at night, turn on many bright lamps over the vessel and wait for the squid to gather, when jigging begins (Arnold 1981; Hamabe et al. 1982). Arrangement of the lights is critical, as this species has a distinct preference for specific light intensities. Lights are hung some distance above deck along the main longitudinal axis of the vessel, with a large vessel using up to 200 kW. Total wattage is regulated by local fisheries agencies (Miyazaki 1971; Flores 1972). Jigging is most productive at the interface between the vessel's shadow and the lighted area of the water column (Sidel'nikov 1981). Larger vessels use motorized jigging machines, with a line 50–200 m long having 50–70 jigs at approximately 80 cm intervals and a lead sinker at the bottom. The length of line to the first jig can be adjusted to stay in the squid concentration (Nedelec 1975; Ben-Yami 1976).

The inshore angling fishery for cephalopods has experienced large fluctuations in the last 30 yr (Fig. 1). Domestic landings reached a maximum of 668 295 t in 1968 and have been decreasing since then (Osako and Murata 1983). The peak in 1968 and two other local maxima in 1952 and 1962–63 correspond to major increases in effort or improvements in gear technology. The resource has probably been maximally exploited around Japan since 1971 (Osako and Murata 1983). Although the Chinese are not believed to utilize this resource to any significant degree (Chikuni 1983), South Korea lands 40 000–80 000 t annually (Worms 1983; FAO 1984). Years of low catches, and introduction of the 200-mile (322 km) exclusive economic zone (EEZ) restricting Japanese operations overseas, have encouraged prospecting for new fishing grounds and resources.

Todarodes pacificus was traditionally dried (surume), but is now also marketed fresh, processed as saki-ika, frozen, and canned.

The *Todarodes* fishery was free of regulation until 1969, when vessels of more than 100 t became subject to approval and licensure by the Ministry of Agriculture and Forestry (now the Ministry of Agriculture, Forestry, and Fisheries). In 1972 these large boats were prohibited from fishing in most of the waters adjacent to Japan, including much of the Sea of Japan, and medium scale vessels (30–100 t) were prohibited from jigging in certain coastal areas. Larger vessels have thus been gradually forced into overseas fisheries. Important concentrations (annual catches of 40 000–70 000 t) of *Todarodes* were discovered off the coast of Sakhalin in 1965, but these became inaccessible after the USSR imposed a 200-mile EEZ in 1977 (Osako and Murata 1983).

In 1973 approval and licensing requirements were extended to medium-sized vessels. Fishing was also prohibited in March and April to prevent wastage of undersize squid (Kasahara and Nasumi 1976; Court 1980). Since 1973 most smaller vessels (5–30 t) have become subject to regulation of the prefectural fisheries associations. Some decrease in number of vessels has occurred, but competition is still intense. Catch per vessel has declined and become variable. The *Todarodes* resource around Japan is believed to have been fully utilized since 1971 (Kasahara and Nasumi 1976; Osako and Murata 1983).

Forecasts of stock size are now made twice yearly on the basis of data collected on larval abundance in waters around southwestern Japan, juvenile and adult abundance in the Pacific and Sea of Japan, oceanographic conditions, and catch statistics (Araya 1976; Osako and Murata 1983). However, these surveys do not have consistent access to waters near Korea, where significant spawning is believed to occur, thus preventing a comprehensive accounting.

The winter subpopulation appears to have a 9-yr (and 27-28-yr) cycle of abundance correlated with oceanographic conditions (Kitano 1979). A positive correlation has also been noted between the index of larval abundance and catch of the winter subpopulation on the Pacific coast of Japan (Watanabe and Okutani 1974; Yasui 1976). Spawner-recruit relations for the winter subpopulation were worked out by Okutani and Watanabe (1983), with spawning stock size predicting the next year's larval abundance with a regression coefficient of 0.63 ($P<0.01$). Accuracy of prediction seems to be limited by absence of environmental and ecological terms in the model. Jigging surveys have been used to predict stock size later in the season, as well as fishing grounds and total yield. Correlations range between 0.80 and 0.99 for yield and stock size or density index (Murata 1983b).

Modelling of mortality, CPUE, and putative stock size (Osako and Murata 1983) showed that the stock was probably overfished beginning in 1959, and that reduced fishing pressure in the last few years has allowed recovery. Maximum sustainable yield was estimated at no more than 400 000-500 000 t annually (Osako and Murata 1983), with annual fishing mortality of 0.1 (Doi and Kawakami 1979). The suggestion has been made to delay fishing of the North Pacific population until August and September in order to derive maximum biomass yield (Shingu et al. 1983).

Ommastrephes bartrami

The fishery for another ommastrephid squid, *Ommastrephes bartrami*, is the result of Japanese exploration following collapse of the *Todarodes* fishery. It is an epipelagic cosmopolite in warm oceanic waters (antitropical), and is maximally abundant at the Subarctic Boundary in summer and autumn, primarily east of 170°E and west of 156°E (Osako and Murata 1983). It performs diel vertical migrations from about 400 m to the surface at night.

Nesis (1973) considered *Ommastrephes bartrami* to be generally limited to waters of 16°C or higher. It was taken in waters as cool as 10.7°C by T/V *Oshoro Maru* in 1978, and as cool as 12.4°C in 1979, with the catch roughly proportional to temperature (Faculty of Fisheries, Hakodate 1979, 1980). Fiscus and Mercer (1982) reported collections at 9.8-9.9°C and 12°C. Naito et al. (1977a) listed its temperature range as 8-24°C, with abundant captures at 12-18°C. Kubodera et al. (1983) showed good correlation between catches and oceanographic conditions, with catches in May above 11°C, in June at 9-18°C, in July at 9-21°C (greatest abundance at 19-20°C), and in August above 15°C.

Adults eat small fish (*Diaphus coeruleus, Engraulis japonica, Sardinops melanosticta, Hygophum, Symbolophorus, Lampanyctus, Nansenia, Scopelosaurus, Centrobranchus, Cololabis saira*, and young *Scomber japonicus*), and other *O. bartrami, Abraliopsis felis*, and *Watasenia scintillans*, but rarely Crustacea. Immature individuals eat euphausiids and *Parathemisto* as well as small fish and squid (Fitch, in Wormuth 1976; Naito et al. 1977b; Bernard 1981; Araya 1983). Its diet indicates that *O. bartrami* probably occupies a higher trophic level than *Todarodes pacificus*. Predators include large fish such as tunas, and marine mammals, especially *Physeter macrocephalus* (Okutani et al. 1976; Okutani and Satake 1978; Bernard 1981).

Ommastrephes bartrami, like *Todarodes*, reaches maturity in about 1 yr and undertakes feeding migrations (Fig. 3). The western subgroup spawns in the Kuroshio countercurrent area during January to May (Araya 1983; Osako and Murata 1983). Larvae have been taken from the coastal area of the Kuroshio near Izu Island from March through May (Murakami 1976a). Young and immature *O. bartrami* of the western subgroup move north with the Kuroshio during May to August. Large schools aggregate in the frontal area at the northern rim of the transition zone off northeastern Honshu, where the Kuroshio meets the Oyashio (Tung 1981). Adults begin a southward migration in October, with most individuals migrating during November to February.

The oceanic portion of the population migrates north to the Subarctic Boundary, concentrating at the transition zone between subarctic and subtropical waters in July (Mishima 1981; Mishima et al. 1981; Kubodera et al. 1983). The southward migration begins in September and October. Four size groups are apparent; the largest (34-38 cm DML) in the transition zone, and the smaller (15-25 cm, peak at 20 cm DML) in subtropical waters. The largest group is exclusively female, smaller groups about equal numbers of males and females; all groups were immature in July (Kubodera et al. 1983). Size groups may result from different maturation rates (Murakami et al. 1981). Most females and all males probably mature at about one year, to mate and spawn in winter and spring in southern Subtropical waters. Some females hatched late in the spring probably live for more than 1 yr, migrating north before young-of-the-year. The large size group found at the Subarctic Boundary in July thus consists of females in their second year. In both subpopulations (Kuroshio and oceanic), males mature earlier than females, and initiate the southward migration. Larger individuals migrate before smaller ones of the same sex.

In 1975 a large resource of *Ommastrephes bartrami* was discovered along the northern extremity of the Kuroshio, resulting in the development of a jig fishery (Anon. 1982). Landings were more than 84 000 t in 1976. This species seems to be more available to jigs than *Todarodes*, and has become much more important in terms of landings since catches of *Todarodes* began to decline in the late 1960s (Okutani 1977). By 1978 *O. bartrami* accounted for nearly half the squid caught in Japanese waters (Fig. 1).

The jig fishery operates in much the same manner as the *Todarodes* fishery, although with a later season (July to December, Osako and Murata 1983). Larger jigs are generally used, and a greater portion of the catch is taken by hand jigging. Optimum fishing grounds change with water temperature and season, beginning around 40°N, 152–160°E in July, and expanding to 40–46°N, 143–165°E as the season advances. By November–December, the fishing grounds have begun to shrink, and centre in the area west of 150°E. This cycle seems to follow the Kuroshio in early summer north to the Subarctic convergence, and to move south with development of the Oyashio in autumn (Murata et al. 1983). Jigging may damage significant numbers of squid which drop off the jigs (e.g., Robinson and Jamieson 1984; Sloan 1984); this does not appear to significantly affect mortality (Murata et al. 1981). Jigging for this species does not appear to be economically feasible in the northeastern Pacific (Mercer and Bucy 1983; Robinson and Jamieson 1984; Sloan 1984).

Development of gillnetting technology for squid in 1978 prompted an expansion of effort into central northern North Pacific waters, followed by an explosive increase in effort to over 1000 vessels, making this the most important Japanese offshore fishery. Initially, this represented merely an incidental catch or a shift in effort by salmon gillnetters after the close of the salmon season, but soon became the primary target of squid fishermen. The much greater efficiency of gillnetters quickly led to significant conflict between them and the jiggers, and to fishery restrictions in 1981.

Although labour- and capital-intensive, the gill net method is quite simple, and takes advantage of the fact that schools of *Ommastrephes bartrami* congregate at the surface at night. Large vessels (approximately 500 t), with significant fuel and labour costs, deploy great quantities of net each fishing day. Individual 8 by 50 m panels ("tans") are strung together in lengths of 15–45 km. Commercial mesh size is restricted to 100–135 mm (Fisheries Agency of Japan 1982). Nets may be set at the surface or sunk to depths up to 10 m and are set before dusk and retrieved before dawn. Up to 30 crew may be required to remove and process the catch, stack and repair the net (Bernard 1981; Osako and Murata 1983; Sloan 1984; a different method is described in Anon. 1982). Kubodera and Yoshida (1981) discussed mesh selectivity. Robinson and Jamieson (1984) demonstrated that green monofilament nets caught two to three times as many squid as white nets. Most catches occurred in 48–157 mm meshes, with peak catches at 121 mm (Kobodera et al. 1983).

Gillnetting grounds shift from 38–39°N, 170–175°E early in the season to 49°N, 160°W at the peak of the season, from June to October (Osako and Murata 1983). In the more northerly grounds, catches of 10 $t \cdot d^{-1}$ are fairly common. Average catch rate is about 5 $t \cdot d^{-1}$ (Anon. 1982), which is the break-even point for a vessel of 50 m and 30 crew (Bernard 1981). Recent work (Sloan 1984) indicates that the break-even point should be increased to 10 $t \cdot d^{-1}$.

Gillnet bycatch is primarily *Brama japonica* (pomfret), *Prionace glauca* (blue shark), and *Lamna ditropis* (salmon shark) (Bernard 1981; Fisheries Agency of Japan 1983; Robinson and Jamieson 1984; Sloan 1984). Shark bycatch increases during daylight hours, thus the necessity for hauling at dawn. Bycatch of tuna and jellyfish increases dramatically in water whose temperature is above 15°C, and of salmonids below 13°C. The preferred surface temperature when targeting *O. bartrami* is 14.5°C (Bernard 1981).

Exploratory fishing for *O. bartrami* has been conducted off the west coast of Vancouver Island (Bernard 1981; Robinson and Jamieson 1984; Sloan 1984). Catches were large enough to justify commercial exploitation, but no fishery has yet developed. Complicating factors include the likelihood of a short season which would conflict with the salmon season, and the relatively glutted squid market.

Although the tissue is highly palatable, most catches of *O. bartrami* are frozen for further processing. Most is converted to surume (dried) or duruma (dried and seasoned) (Bernard 1981). There is significant interest in the United States in markets for such processed squid (Flanagan 1983).

The *Ommastrephes* fishery was first regulated in 1979 after much conflict between jigging and gillnetting vessels the previous season. Gillnetters are much more efficient than the jiggers, with catch rates up to ten times those of the jiggers (Osako and Murata 1983), and significantly lower fuel consumption, but jig fishermen claimed economic dependence on the fishery and priority (Court 1980). In 1979 the Fishery Agency prohibited gillnetting for squid in the area north of 20°N and west of 170°E (Court 1980). In 1981 the Fishery Agency limited drift gillnetting for squid to the offshore area between 20° and 46°N, and between 145°W and 170°E (outside the U.S. 200-mile (322 km) EEZ around the Hawaiian Islands — Fig. 3). Drift gillnet vessels have been limited by size (50–500 t), number (limited permits

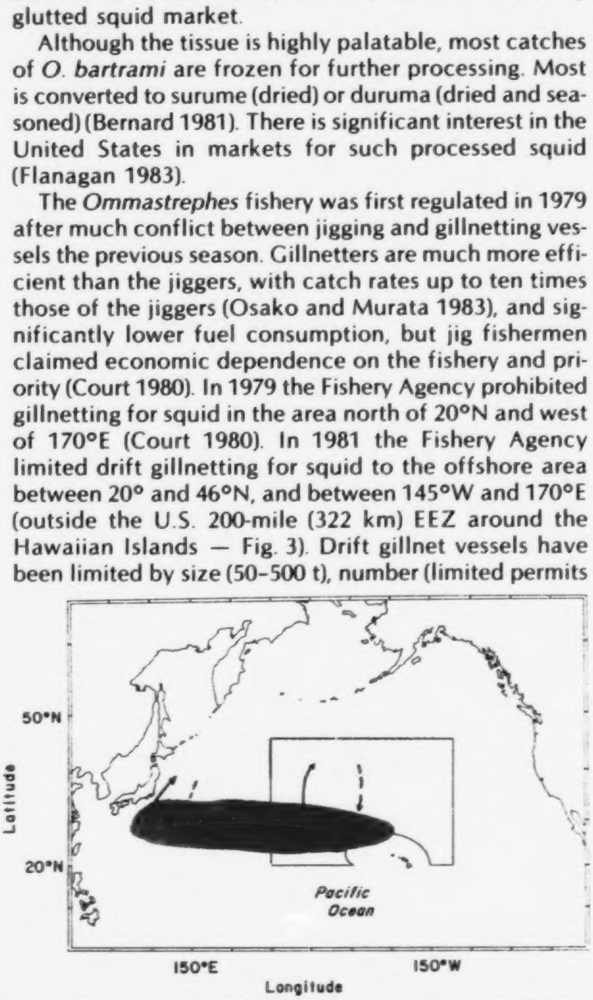

FIG. 3. *Ommastrephes bartrami* in the North Pacific: fishing grounds (light hatching — gillnets allowed only within box around Hawaiian Islands); spawning grounds (vertical hatching); and migration routes (arrows), north in spring–summer and south in autumn. Data from Anon (1982), Murata (1983b), and Osako and Murata (1983).

issued by Minister of Agriculture, Forestry, and Fisheries), and equipment (blast freezing capacity of 4–10 t per 24 h) (Anon. 1982; Court 1982; Osako and Murata 1983). Mesh size must be at least 10 cm, and the season has generally been limited to the second half of the year (Court 1982).

Forecasts of stock size and fishing grounds are made twice yearly for *O. bartrami*, using data on larval abundance, oceanographic conditions, and catch statistics (Murata 1983b; Osako and Murata 1983). It is likely that stocks fished by jigging have been fully exploited since about 1978, resulting in a recent decline both in average mantle length and in stock size (Araya 1983; Osako and Murata 1983). Fishing mortality has been estimated at over 30% (Murata and Shimazu 1982). Osako and Murata (1983) postulated MSY at a level of 80 000–100 000 t annually, for stocks fished by jigging. Attempts to correlate stock size with research jigging CPUE have not been successful, probably because the research covered only a portion of the distribution (Murata 1983b).

Management recommendations for a potential gillnet fishery in the northeast Pacific included location directives (more than 100 km offshore, above 13°C), gear restrictions (maximum 30 km net), and bycatch limitations (salmon under 1% by weight, tuna under 5%) (Bernard 1981).

Dosidicus gigas

Another ommastrephid squid, *Dosidicus gigas*, is believed to form a significant, and largely unexploited, stock in the eastern Pacific (Okutani 1977). It is harvested, at least occasionally, from southern California to Isla Chiloe off central Chile (Nesis 1970; Sato 1976; Castellanos and Cazzaniga 1980; Hochberg and Fields 1980; Hochberg 1981; Roper et al. 1984) (Fig. 4). This species is closely associated with regions of upwelling and high productivity (Nesis 1970; Klett 1982). Temperature preference seems to be 15–28°C (Nesis 1983). Japanese work off Baja found greatest concentrations over the continental slope, especially in convergences (Sato 1976). Diurnal vertical migration occurs, with adults moving into the upper 100 m at night. Seasonal migrations occur in the Gulf of California, with animals moving into the Gulf of California in winter, and reaching a northern limit of 29°N in April. In August and September, southward migration begins, but a small portion of the stock remains in the upper central portion of the Gulf. The group reaching the south splits into two subgroups, of which one moves south along the coast, and the other moves slightly offshore north of the mouth.

In and near the Gulf of California, spawning appears to occur in three peaks: winter, with recruitment in March–April; late spring–early summer, with recruitment in September; and late summer–early autumn, with recruitment in January–February. Most winter spawning occurs in the Pacific off the mouth of the Gulf, and summer spawning appears to occur in the west central Gulf. Growth rates are extremely rapid, up to 8–9 cm·mo^{-1} in the first 4–5 mo. Lifespan in the Gulf populations is 18–20 mo. Standing stock has been estimated at 13 500 t in the Gulf of California in May, obviously with high turnover (Ehrhardt et al. 1983b).

Populations off South America may live somewhat longer, 3–4 yr, with lower growth rates, 2–2.5 cm·mo^{-1} in the first year (Nesis 1970). Growth rates in all populations are probably temperature-dependent. Spawning probably occurs in the southern hemisphere in spring and summer over or on the continental slope (Nesis 1983). Southern populations also migrate from the spawning area westward and toward the equator, as they grow moving back into more productive areas in the equatorial zone and in the Peru Current. Large spawning migrations take place from October to December (Nesis 1983).

The diet is size-dependent, changing from crustaceans in small individuals to fish and then squid, including *D. gigas*, in the largest individuals (Ehrhardt et al. 1983b). Fish species consumed include *Sardinops sagax caeruleus, Scomber japonicus, Myctophum aureolaternatum, Symbolophorus, Hygophum atratum, Lampanyctus parvicauda, Diogenichthys laternatum, Benthosema panamensis, Scomberesox saurus*, Exocoetidae, *Vinciguerria lucetia, Genypterus, Merluccius*, Carangidae (Fitch 1968; Nesis 1970, 1983; Ehrhardt et al. 1983a,b). Other items include *Pleuroncodes planipes*,

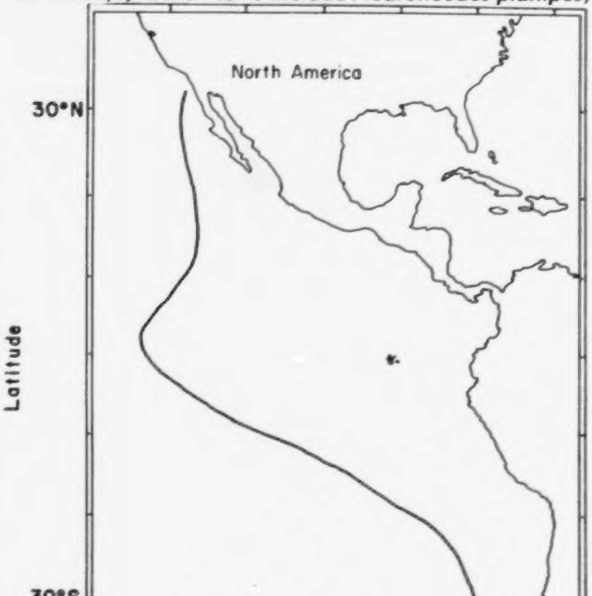

FIG. 4. Distribution of *Dosidicus gigas* (east of heavy line), and major fishing area (light hatching).

decapods, and stomatopods (Sato 1976; Nesis 1983; Ehrhardt et al. 1983b). Predators include *Physeter macrocephalus, Coryphaena hippurus, Neothunnus macropterus, Makaira mitsukurii*, pilot whales, sharks, tunas, marlins, swordfishes, and *D. gigas* (Wormuth 1976; Nesis 1983).

The fishery for *Dosidicus gigas* began as an artisanal one in 1974. Rapid expansion of effort by shrimpers began in 1978, and the Japanese and Koreans began joint-venture operations in 1979. In 1980 the fishery expanded to year-round operations, with peak landings of 22 000 t (Hochberg 1981; Klett 1982). Landings have since declined to 6634 t in 1982 (Ehrhardt et al. 1983a,b; FAO 1984). Most landings occur from April to October, with a peak from May to July (Klett 1982). The fleet consists of 15 large jigging vessels, about 200 local boats which transfer from the shrimp fishery, and a few dozen small open boats. All vessels use jigs under lights (Ehrhardt et al. 1983b). The fishery off South America is an artisanal one (Nesis 1983).

The Mexican Department of Fisheries has estimated the potential harvest of this species off Baja as about 300 000 $t \cdot yr^{-1}$ (Juanico 1982). It is marketed frozen in the U.S. under the name "grande calamari" as an abalone substitute (Blake 1982; Dewees and Price 1982). Nesis (1983) estimated total annual production for this species at about 1–1.5 million t. The southern fishery uses this species fresh, canned, and for reduction to meal (Nesis 1983; Roper et al. 1984).

OTHER OMMASTREPHIDS

Symplectoteuthis oualaniensis occurs throughout the entire subtropical and tropical Indo-Pacific. Rhynchotheuthion larvae of this species are abundant in summer between Taiwan and the southern Japanese islands, in the South China Sea, and also offshore in the Pacific (Shojima 1972; Yamamoto and Okutani 1975; Tung 1976). *Symplectoteuthis oualaniensis* is important in the diets of several birds, including the booby, white-capped noddy (Voss 1954), and *Sula piscator* (Hoyle 1886, 1904; Clarke 1966).

This species is commercially exploited only in Okinawa and Taiwan, although it is apparently also jigged for tuna bait around Hawaii (Okutani and Tung 1978; Chikuni 1983; Roper et al. 1984). Commercial landings are 300–400 $t \cdot yr^{-1}$ (Okutani and Tung 1978). This species is difficult to concentrate under lights; discovery of a more appropriate fishing technique may be necessary to fully exploit it. A large stock is believed to exist; Voss (1973) estimated 100 000 t.

Symplectoteuthis luminosa occurs across the North Pacific in transitional and subtropical waters. Males grow somewhat larger than the females (Clarke 1966). This species does not form large schools (Hamabe 1978), and is reported to occur at 19.5–21.5°C (Kubodera et al. 1983). It is occasionally taken in jig and gillnet fisheries for *T. pacificus* and *O. bartrami* (Kubodera et al. 1983; Roper et al. 1984).

Potential harvest of two other ommastrephids, *Nototodarus hawaiiensis* and *Nototodarus philippinensis*, (Table 4) is believed to be quite large (Roper et al. 1984).

OTHER OEGOPSID FISHERIES

Three other oceanic species are of growing interest to the North Pacific Japanese fishing industry: *Onychoteuthis borealijaponica* (Onychoteuthidae), and *Gonatopsis borealis* and *Berryteuthis magister* (family Gonatidae). *Onychoteuthis* is both gillnetted and jigged, primarily off eastern Hokkaido, *Gonatopsis borealis* is taken in gillnets, and *Berryteuthis* is generally taken in bottom trawls (Murakami 1976a).

Onychoteuthis borealijaponica is a common epipelagic species throughout the North Pacific except in the central water mass (Fig. 5), where it is largely replaced by *O. banksi* (Okutani 1977; Jefferts 1983). *Onychoteuthis borealijaponica* is absent from the Sea of Okhotsk, most of the Bering Sea and Gulf of Alaska, even in summer. Females are 3–4 cm larger than males, on average, and there is some indication that the largest individuals migrate farthest north (Kubodera et al. 1983). Prey includes euphausiids, amphipods, small fishes, and squid of its own species (Murata 1983b; Okutani and Murata 1983).

Onychoteuthis borealijaponica migrates north in summer to the southern edge of the Subarctic water mass near the southern Kuriles, and south in winter to warmer water (Murata et al. 1976; Murakami 1976a,b). This species is most abundant in May at 4–11°C, in June at 6–17°C, in July at 6–16°C (most abundant at 10–12°C), and in August at 8–14°C (mostly < 11°C, Kubodera et al. 1983; also, Naito et al. 1977a; Fiscus and Mercer 1982). It is generally found in western Subarctic waters in summer, and less often in transitional waters, with especially high catches where the thermocline is shallow below 10–11°C surface waters. Northern migration may be limited by the 6–7°C isotherm (Kubodera et al. 1983).

Larvae are abundant in winter at depths of 80–200 m, and probably mature after August to spawn the following autumn and winter (Fiscus and Mercer 1982; Kubodera et al. 1983; Okutani and Murata 1983). This species begins to recruit to the fishery in June and July, reaching peak abundance in late summer. The southward spawning migration begins in fall with maturing males, followed by larger females. The entire stock has moved south by late fall to spawn in warm waters of

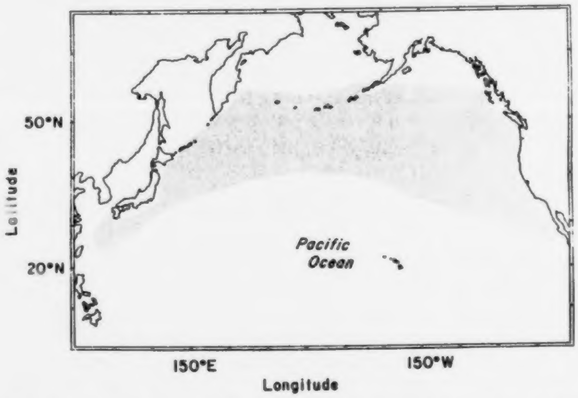

FIG. 5 Distribution of *Onychoteuthis borealijaponica* (light hatching).

the Kuroshio countercurrent (Kubodera et al. 1983; Osako and Murata 1983). It is not known whether other spawning grounds occur in the central or eastern Pacific.

This species is primarily taken incidental to the jig fisheries for *T. pacificus* and *O. bartrami* off the eastern coast of Hokkaido, and in the gillnet fishery for the latter near 180° (Kubodera et al. 1983). Landings have varied between 0 and 2200 t in the last 15 years (Table 3; Okutani and Murata 1983). Experimental jigging for *O. borealijaponica* off the British Columbia and Washington coasts did not result in commercial quantities (Bernard 1980; Mercer and Bucy 1983), but the authors felt such a fishery might be economically feasible in times of upwelling. Gillnet catches are three to four times higher than for *Gonatopsis borealis*; it is most often taken in 48-82 mm meshes, with peak catches at 63 mm (Kubodera et al. 1983).

Jigging surveys are conducted in the northwestern Pacific to forecast stock size of *Onychoteuthis borealijaponica*; no other management takes place. Attempts to relate stock size to yield have been unsuccessful, probably because the survey does not cover the entire distribution of this species (Murata 1983b). Potential catch is estimated at 50 000-200 000 t (Murata, in Okutani 1977).

Gonatopsis borealis is found primarily in the Subarctic water mass, with occasional occurrences in transitional and northern central waters (Jefferts 1983; Kubodera et al. 1983) (Fig. 6). Longevity is estimated at one year, with growth slowing noticeably after sexual maturity is reached (Naito et al. 1977b; Okutani and Satake 1978). This species apparently occurs as two populations, divided by the size at maturity (below or above 190 mm DML; Naito et al. 1977a). In the central North Pacific, only the smaller group (110-180 mm DML) occus in the Subarctic west of 165-170°E. East of 167°E, the larger group (200-270 mm DML) occurs south of 47°N, and the smaller group north of 47°N (Kubodera et al. 1983). The large group also occurs off the southern to middle Kuriles (Naito et al. 1977a).

Gonatopsis borealis does not undertake feeding and spawning migrations like those of the warm water *T. pacificus* and *O. bartrami*, but its distribution moves northward somewhat with summer warming. In the northeastern Pacific, it is found generally north of 50°N in summer, and in the northwestern Pacific, generally north of 44-45°N (Kubodera et al. 1983). In the northwestern Pacific it appears in April, becoming more abundant and widely distributed by June-July. Although frequently encountered, it is apparently never present in large schools (Kubodera et al. 1983).

This species migrates vertically between 400-700 m in the daytime and the upper 400 m at night (Roper and Young 1975). Predators include *Callorhinus ursinus* (Laevastu and Fiscus 1978; Fiscus 1984), *Phocoenoides dalli* (Kajimura et al. 1980), *Lagenorhynchus obliquidens* (Stroud et al. 1981), *Physeter macrocephalus* (Rice 1963; Okutani and Satake 1978), and *Mirounga angustirostris* (Antonelis and Fiscus 1980).

Kubodera et al. (1983) showed that this species was taken in May at 2-8°C, in June at 3—11°C, in July at 5-13°C, and in August at 8-14°C, in significantly colder waters than *O. borealijaponica* and O. bartrami. It has been taken year round in gillnets in the northeastern Pacific, in water as cold as 3.4-4.4°C (Fiscus and Mercer 1982).

This species is an incidental catch in the jig fishery for *Todarodes pacificus* off northeastern Honshu and Hokkaido (Okutani 1977), and in the gillnet fishery for *Ommastrephes bartrami*. Largest catches are made from the southern Kuriles to the Kamchatka Peninsula, and near 46-47°N, 175°E (Osako and Murata 1983). In experimental gillnet fishing, *G. borealis* was taken most often in 48 and 55 mm meshes (Kubodera et al. 1983).

Berryteuthis magister is abundant in the Subarctic Pacific from the Sea of Japan to California, including the Bering Sea and Bering Strait (Jefferts 1983) (Fig. 7). It is unusual in that larvae are epipelagic but juveniles and adults are nektobenthic from 200 to 1000 m (Roper and Young 1975). It probably matures in about 1 yr.

Immature individuals eat only Crustacea (euphausiids, *Parathemisto*, calanoids), while adults eat only small fish and squid (Naito et al. 1977b). This species is important in the diets of *Physeter macrocephalus* (Beteshava and Akimushkin 1955; Akimushkin 1963; Okutani and Nemoto 1964; Okutani et al. 1976), *Callorhinus ursinus* (Panina 1964; Fiscus et al. 1965), albatrosses (Sasaki 1920), and salmonids, which prey heavily on juveniles (Oako and Murata 1983).

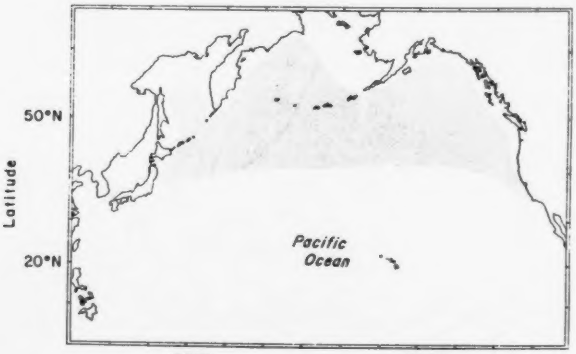

FIG. 6. Distribution of *Gonatopsis borealis* (light hatching).

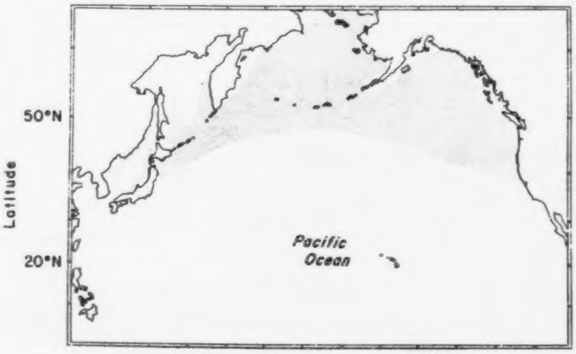

FIG. 7. Distribution of *Berryteuthis magister* (light hatching).

This species shifts to a benthic habit before sexual maturity and spawns on the continental slope between 200 and 500 m, from June to October, in the Commanders, Attu Island, the Japan Sea and Tohoku region (Naito et al. 1977a).

North of the Kuriles, the fishing season lasts from July to October and concentrates on mature stocks. An experimental trawl survey in the Japan Sea caught this animal in all bottom trawls between 250 and 1200 m; over 38 t were taken (Ogata et al. 1973). An otter trawl fishery for this species began in the northeastern Pacific and Bering Sea in the late 1970s. Japanese landings have been 5000–9000 t (Sato and Hatanaka 1983), but the Soviet fishery on redfish in the Bering Sea probably also takes significant quantities (Roper et al. 1984).

Berryteuthis magister is occasionally taken in high seas gillnets, primarily from May to July, at 6–13°C (Kubodera et al. 1983). Although abundant, this species will probably remain a latent resource until processing difficulties due to high water content are overcome.

Two other species are of much less importance, but are presently the object of small fisheries in the North Pacific: *Thysanoteuthis rhombus* (Thysanoteuthidae), and *Watasenia scintillans* (Enoploteuthidae).

Thysanoteuthis rhombus forms only relatively small groups rather than schools. Predator include blue marlin (Voss and Erdman 1959) and sperm whales (Roper et al. 1984). This species migrates into the Japan Sea with the Kuroshio and Tsushima currents from the south when the temperature exceeds 19°C (Nishimura 1964). Migration usually begins during late May and June.

A jig fishery has existed in the Japan Sea since 1962, with annual catches of 0–620 t (Table 3). The fishery is conducted by about 200 small boats, which jig both day and night. This species is also fished with bait (*T. pacificus*) and trap nets off the west coast of Honshu (Hamabe 1978; Osako and Murata 1983). Peak catches occur from September to November, in years when the temperature at 100 m is greater than 17°C (Osako and Murata 1983).

The only regulation of the *Thysanoteuthis rhombus* fishery is a gear directive: not more than 30 units of gear (jigging lines or traps) per boat (Osako and Murata 1983). The resource in the Japan Sea is thought to be controlled more by oceanographic conditions than by harvesting levels.

Watasenia scintillans occurs in deep water (200–600 m) offshore, but spawns in shallow water in Toyama Bay, forming large schools. The life span is believed to be 1 yr. Eggs probably belonging to this species appear in March to August at 10–27°C (Shimomura and Fukataki 1957). These are among the few known pelagic squid eggs (Arnold and Williams-Arnold 1977). Important predators include baleen whales (Nemoto 1957), *Callorhinus ursinus* (Wilke and Kenyon 1954) and *Theragra chalcogramma* (Shimomura and Fukataki 1957).

This species has been the subject of a fishery since at least the turn of the century. It is fished only in Toyama Bay, with set nets from mid-February to early July (peak April and May). Recent annual landings have been 900–3700 t (Okutani 1977; Osako and Murata 1983).

LOLIGINID FISHERIES

Loligo opalescens is a neritic species occurring from the southern end of Baja California to southeastern Alaska, although essentially all landings have been in California until the last few years (Fig. 8). It has a life span of 1–2 yr. (Hixon 1983).

This species migrates into shallow water to spawn (usually at 5–40 m, although eggs have been taken as deep as 100 m — Dewees and Price 1982; Schones 1984). Most known spawning locations are in sheltered inshore sites with sand and mud bottoms. The fishery takes advantage of pronounced seasonal peaks, beginning in early winter in southern California, and moving gradually northward until late summer (Table 5). Information about spawning in Alaska is drawn from data from a portion of 1 yr; spawning squid were observed from April through June, but anecdotal information indicates the spawning season may begin as early as December or January (Street 1982). Hatching time of eggs is temperature dependent, requiring from 12 to 23 d at 16°C, to 90 d at 7–8°C (Table 5). Egg predation is relatively minor, but includes consumption by the echinoderms *Patiria* sp. and *Lytechinus* sp. (MacGinitie and MacGinitie 1968).

Unknown at this time is whether this species is represented by more than one stock; work on this problem has so far been inconclusive (Kato and Hardwick 1975; Kashiwada and Recksiek 1978; Ally and Keck 1978; Christofferson et al. 1978). This species schools by size, and is most abundant at 10–16°C (Roper et al. 1984).

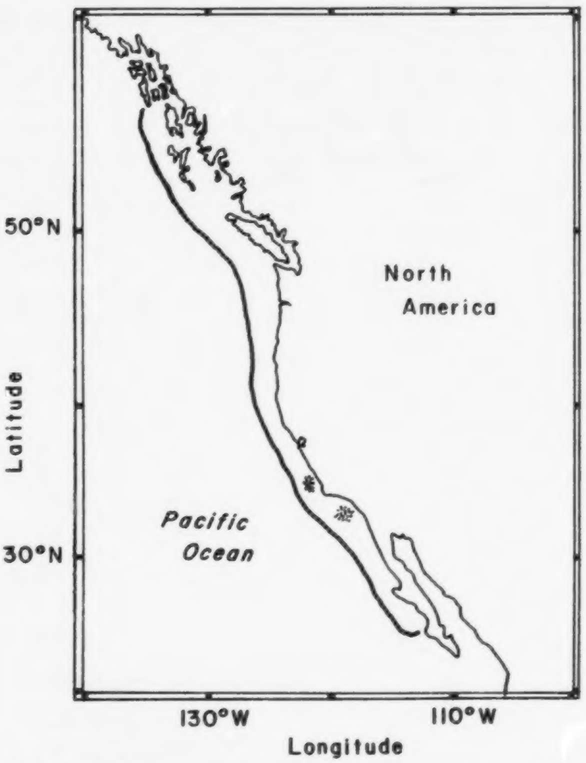

FIG. 8. Distribution of *Loligo opalescens* (east of heavy line) and location of fishery efforts (light hatching).

TABLE 5. Spawning seasonality and hatching time in *Loligo opalescens*. (Macfarlane and Yamamoto 1974; Kato and Hardwick 1975; Recksiek 1978; Spratt 1979; Bernard 1980; Morris et al. 1980; Fisher 1981; Street 1982).

MAIN SPAWNING SEASONALITY	
SE Alaska	May to June
British Columbia	July to late summer
Washington	July to September
Oregon	April to July
Monterey	May to June; November
Southern California	December to March; occas. July
HATCHING TIME	
British Columbia	
7–8°C	90 d
10°C	70 d
California	
13.6°C	30–35 d
16°C	12–23 d

Prey items are mostly euphausiids, but may also include fish and their own species (Loukashkin 1976; Karpov and Cailliet 1978, 1979); feeding rate has been estimated at 14% body weight per day (Karpov and Cailliet 1978). This species is important in the diets of salmonids, flatfishes, other fish, sharks, marine mammals, and birds (LeBrasseur 1965; Pinkas et al. 1971; Morejohn et al. 1978; Stroud et al. 1981; Hixon 1983; see summary in Jefferts 1985).

The fishery began in Monterey in the 1860s when Chinese fishermen rowed about the bay with torches in the bows of their skiffs, setting a purse seine around the aggregated squid (Collins 1892). In 1905 the Italians introduced a lampara seine — which has remained the gear of choice in Monterey — capable of catching several tons in one set (Frey 1971). Several hundred tons were harvested annually and dried for export to the Orient. Processing changed through introduction of canning and freezing techniques in the 1920s, and the closure of the Oriental market in 1933. Catches remained at much the same level until after World War II, when suddenly increased demand for U.S. foreign aid programs prompted annual landings of 9 000–18 000 t (Frey 1971) (Fig. 9). The Monterey fishery usually occurs from April to September.

The southern California fishery for *Loligo* began in the 1950s, using nightlights and a power-assisted lift net (lamparas and purse seines are also employed). The fishery occurs from December to April, with peak landings in January, which usually derive from concentrations in the Channel Islands (Dewees and Price 1982). Processors have traditionally paid higher prices for Monterey squid, and for squid destined for freezing. Until recently annual landings have been 10 000–20 000 t for all of California (Anon. 1983).

The southern California fishery has also experimented with a pump system for harvesting squid; trials of this gear showed a potential for taking over 45 t per night (Kato 1970). This method is only effective for squid which can be concentrated under lights; it may or may not be effective for squid fishing farther north along the coast. Demersal trawling is effective only in the daytime, when the squid tend to concentrate on the bottom, and at relatively high speeds — 5.6–8.3 km·h⁻¹.

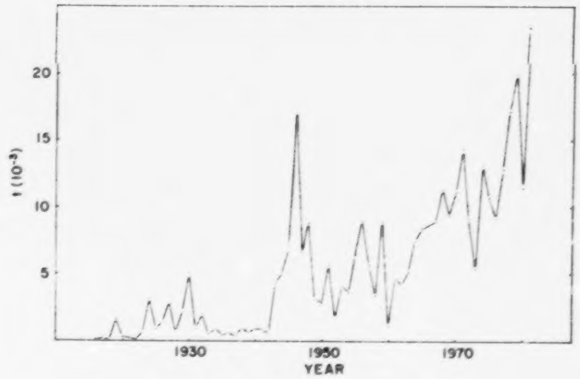

FIG. 9. Landing (t) of *Loligo opalescens* in California, 1916–82. Data from Classic (1929), Fields (1950), and Anon. (1983).

Estimates of the potential yield of this stock range from 100 000 t (Voss 1973) to 300 000 t (Gulland 1971). Spawning concentrations are known which are not or only lightly utilized (e.g., Mais 1974; Macfarlane and Yamamoto 1974; Bernard 1980). The recent El Niño event was associated with drastic reductions in the California fishery and prompted exploration in northern California and Oregon. Oregon landings have increased dramatically in the last two years: from 51 t in 1982 to 428 t in 1984 (Starr 1983, 1984; Starr and McCrae 1984a,b). The fishery in Washington has never been large; maximum landings were 95 t in 1941. Landings since 1980 have ranged from 1 to 40 t. Most catches are taken by jigging or with beach seines or dip nets. The British Columbia fishery has been largely a bycatch fishery, although Bernard (1980) indicated a potential for expansion. Likewise, only exploratory fishing efforts have been made in Alaska, with some potential for expansion (Street 1982).

Management of the California fishery has been primarily aimed at preventing damage to benthic egg capsules. Some gear restrictions are in effect, primarily due to efforts of the industry itself. Artificial lights and purse seines are outlawed in the Monterey fishery; the main effect has been to sustain the small-boat nature of that fishery. Attempts to assess the stock biomass have been limited; there is some indication of a correlation between squid availability at Monterey and water temperature 18 months earlier (McInnis and Broenkow 1978). Acoustic methods show some promise for estimating standing stock, especially on spawning grounds (Cailliet and Vaughan 1983; Jefferts et al. 1984).

Management of the fishery in Oregon became an issue only recently. In 1984 a target of 2045 t was set for the fishery state-wide. Permits were required only for trawling; these were issued on an experimental basis, and were limited in number and duration. The only industry-wide regulation was a 9 t trip limit; this was placed with the processors' limitations in mind and to discourage large vessels from outside the state from entering the fishery. Demersal trawlers harvested about one-half the total squid in 1984, lampara seiners about one-third, and purse seiners the remainder.

OTHER LOLIGINID FISHERIES

Japan and other western Pacific nations also exploit a number of species of the family Loliginidae (Table 4). Most species in the family are small in size, and all are neritic, with fairly restricted geographic ranges. Among the smaller species which Japan utilizes are *Loligo japonica* and *L. beka*. Larger species fished by a variety of peoples (or nations) include *Sepioteuthis lessoniana* (Hawaii to the Red Sea and Australia), *Loligo edulis* and *L. edulis budo* (western Japan, South China Sea, Philippines to the Red Sea), *L. chinensis* (Amami group, Taiwan, South China Sea, Australia), and *L. duvauceli* (Taiwan, Indonesia to northeastern Africa); and the smaller *Loligo uyii* (China, Taiwan, Japan), *Doryteuthis reesei* (Philippines) and *D. singhalensis* (Taiwan, Philippines, India, Sri Lanka, Seychelles) (Sasaki 1929, Okutani and Hatanaka 1976; Chikuni 1983). Japan is the only major harvester of the large *Doryteuthis bleekeri*. In the eastern Pacific, *Loligo opalescens* is the only loliginid exploited.

Loligo edulis and *L. edulis budo* are neritic, and perform seasonal onshore-offshore migrations. *Loligo edulis* overwinters in deeper water, migrating onshore to spawn in spring and summer, while *L. edulis budo* grows and matures in shallow water, migrating offshore to spawn in summer to fall. Both lay demersal eggs.

These species are taken in warmer months by several methods; recent annual catches have been about 20 000 t (Okutani 1977; Chikuni 1983) (Table 3). *Loligo edulis* is a major fishery in Hong Kong, amounting to more than 6000 t. That fishery is primarily conducted by pair trawlers. *Loligo edulis* landings in China reach about 6000 t annually (Dong 1981). Both species are processed into dried products (surume), *L. edulis* is also sold fresh for sashimi.

Loligo japonica forms large schools and is fished with set nets and small trawls by Japan and China (Chikuni 1983). China lands several thousand tons annually (Dong 1981). It is primarily used fresh, as sashimi (Hamabe 1978).

Loligo chinensis forms large schools, and can be readily attracted to lights. Landings off Hong Kong may reach 2000–3000 t (Voss and Williamson 1971), and off China about 10 000 t (Dong 1981).

Loligo duvauceli spawns in large concentrations year round, although peaks may coincide with temperature maxima (Chikuni 1983; Roper et al. 1984). Maturity probably occurs at 1–3 yr. This species feeds on planktonic crustaceans, squids (including *L. duvauceli*), and fishes (Roper et al. 1984). It forms large aggregations and can be attracted with light. This species is fished throughout its range, with purse seines in Hong Kong, and with trawls and artisanal methods elsewhere (Chikuni 1983).

Sepioteuthis lessoniana does not form large schools (Hamabe 1978), but can be attracted with light (Chikuni 1983). Prey items include fish and nektobenthic or benthic crustaceans (Roper et al. 1984). This species is fished year round in southeast Asia with a variety of gear (Table 4). It is used both fresh and dried.

Doryteuthis bleekeri occurs in the neritic waters of Japan (southern Hokkaido to southern Kyushu) and southern Korea. It reaches a maximum size of 400 mm DML (Roper et al. 1984). It spawns inshore, laying eggs demersally.

This species was historically fished in Japan with fixed nets and by jigging, but has recently been exploited with blanket nets and bottom trawls. It is fished at all stages of the life cycle. Immature, demersal individuals are taken with trawls from September to November in eastern Honshu; mature males moving inshore are jigged in winter; spawning females are taken by light attraction and set nets in winter and spring; and individuals moving inshore are taken by trapnets in February to July along the coast of Hokkaido (Osako and Murata 1983). Peak landings occur in April and May. Aquaculture feasibility studies are being conducted with this species (Osako and Murata 1983).

CUTTLEFISH FISHERIES

About 20 species of Sepiidae are fished in Japan, primarily by bottom trawling. The rest of the catch is taken incidentally with jigs, small coastal trawls, and trapnets (Osako and Murata 1983). *Sepia esculenta* is the most important species, followed by *S. lycidas* and *Sepiella japonica*. About half the annual harvest comes from the Seto Inland Sea; large quantities also are harvested from the East China and Yellow seas, primarily as bycatch (Okutani 1977; Chikuni 1983). In 1982 the total Japanese catch was 7661 t, down significantly from 25 110 t in 1978 (FAO 1984). The Japanese cuttlefish fisheries are probably underexploited, with the exception of the fishery for *Sepiella japonica*, which is probably overfished between Shikoku and Honshu (Osako and Murata 1983).

Sepia esculenta probably has a 1-yr life cycle, spawning attached demersal eggs from March to July (Hamabe 1978; Osako and Murata 1983; Chikuni 1983), and has been reared in culture (Choe 1966). The life cycle of a similar species, *S. officinalis*, is well known, and described by Boletzky (1983). The fishery peaks during the breeding season, when large aggregations are formed, declines until winter, and then begins to increase in November to January (Chikuni 1983; Osako and Murata 1983). Japan and Korea take 10 000–20 000 t, China 1000–2000 t, and Hong Kong about 100 t annually (Chikuni 1983). The northern stocks have probably been fully exploited since the late 1950s (Chikuni 1983). It is marketed both fresh (for sashimi) and frozen (Roper et al. 1984).

Sepia pharaonis lays demersal eggs, and may live 1–3 yr, males longer than females. It preys on, and is preyed on, by demersal fish. The pharaoh cuttlefish also eats crustaceans (Roper et al. 1984). It is widely fished (Table 4).

Sepiella japonica is taken in the East China Sea and off Honshu and processed into surume (Hamabe 1978; Roper et al. 1984). China takes 30 000–70 000 t annually (Dong 1981). This species has probably been fully exploited since the early 1960s, but no evidence yet exists of overfishing (Chikuni 1983).

In 1982, Japan harvested 42 485 t of octopuses with traps (octopus boxes or octopus pots), bottom longlines, draghooks, jigs, spears, and trawls. There are two distinct octopus fisheries in Japan: a southern coastal (southern Honshu, Shikoku, Kyushu, and the Seto Inland Sea) fishery primarily for *Octopus vulgaris*; and a northern oceanic one (off northern Honshu and Hokkaido) for the large *Octopus dofleini* with lesser quantities of *O. conispadiceus* and *O. araneoides*. Various gear employed in the two fisheries is described by Nedelec (1975), Koyama (1976), and Kelle (1978). Electrical fishing methods are also a possibility (Lamarque 1962). Octopuses are also important components of fisheries in China, Taiwan, Hong Kong, the Philippines (Voss 1973), the Gulf of Thailand, Indonesia, and Malaysia, and may amount to several hundred thousand tons (Chikuni 1983).

Species which are of secondary commercial importance in the northwestern Pacific, including the Sea of Japan and South China Sea, include *Octopus macropus, O. membranaceus*, and *O. variabilis*, as well as several species with more tropical distributions (Table 4). China fishes *O. vulgaris, O. ocellatus*, and *O. variabilis*, and is probably the second largest consumer of octopus after Japan (Wilson and Gorham 1982b). Korea is also an important consumer of octopus; in 1982 that country harvested 21 806 t, from off northwest Africa as well as the North Pacific (FAO 1984).

Octopus vulgaris is a warmwater species, in which feeding behaviour becomes irregular below 12°C, and ceases below 7°C. Spawning off Japan occurs in shallow water over an extended period, with peaks in April–May and September–October. Hatching takes 22–25 d at 25°C, and up to 125 d at 13°C. The hatchlings are planktonic for 5–12 wk, and then take up a benthic existence. Growth rates are rapid, up to 4.5 kg in 8 mo, depending on temperature (Mangold 1983b; see also Wells and Wells 1977). In the Seto Inland Sea, they may reach 1 kg in 4 mo (Roper et al. 1984). The lifespan is believed to be 12–18 mo. Mating may occur 5–8 mo before spawning (Mangold 1983a,b).

Food items include crustaceans, bivalves, fish, polychaetes, and *O. vulgaris*. Young individuals are preyed on by jellyfish, squid, and fishes (*Thunnus alalunga, Trachurus, Pomatomus, Epinephlus, Conger*, serranids, and sparids) (Mangold 1983b; Roper et al. 1984).

The Seto Inland Sea octopus fishery occurs year round, and averages about 9000 t·yr^{-1}. The pot fishery takes about 15% of the catch, trawling 65% and angling 20%. These fisheries occur from late spring to early autumn, while the draghook fishery occurs in autumn. *Octopus vulgaris* is taken at 20–80 m, often on pebble bottom (Itami 1976). This fishery is currently fully exploited; measures to improve recruitment, such as setting out spawning boxes, have been undertaken in the last few years (Anon. 1975; Hamabe et al. 1976b; Okutani 1977). The catch is marketed fresh, frozen, and dried and salted (Roper et al. 1984).

The fishery for *Octopus dofleini* takes advantage of two seasonal migrations from deep (180–200 m) to shallow (10–50 m) water. This species is in deep water from February to April and from August to October (Wilson and Gorham 1982b). Females are inseminated during the onshore, autumn migration. They lay their eggs in shallow water the next spring (May–June), and brood them for 6–7 mo (hatching peak November–December), dying shortly thereafter. Hatchlings remain in the plankton until the following March. Tagging of wild specimens has shown growth from 1 to 10 kg in 1 yr (Wilson and Gorham 1982b); they probably reach 10 kg in 3 yr (Osako and Murata 1983). Females are larger than males of equivalent age (Hartwick 1983; Osako and Murata 1983). This species has a life expectancy of 4–5 yr, but may reach maturity as soon as 1½–2 yr following hatching. Spawning in the northeast Pacific probably peaks in midwinter, and the planktonic stage probably lasts 2–3 mo (Hartwick 1983).

In the northeastern Pacific, prey items include bivalves (*Protothaca staminea, Clinocardium nuttallii, Tresus capax*) and other molluscs, and *Cancer* sp. Predators include *Enhydra lutris, Phoca vitulina, Eumetopias jubata, Mustela vison, Ophiodon elongatus*, other fishes and *O. dofleini* (Hartwick 1983). This species is usually found at temperatures of 7–15°C (Hartwick 1983).

The Japanese fishery began off Hokkaido in 1955, as a substitute for the failing herring fishery (Osako and Murata 1983). It takes *O. dofleini* by three methods from shallow water to 180 m. Draghooks are used in shallow water in winter and spring, while baited or unbaited longlines are set in passes used by migrating octopuses during April–July and November–February. Handlines, using something like squid jigs, are used in shallow to moderate depths, and spears, harpoons, and rakes are used in conjunction with a glass viewing box in shallow water (Sakamoto 1976; Yamashita 1976). Significant quantities are also taken in octopus boxes set on flat bottoms at 40–60 m during May–August and December–February (Osako and Murata 1983). The fishery takes about 20 000 t·yr^{-1} and is probably not overexploited, although it may be susceptible to marine pollution (Okutani 1977; Osako and Murata 1983).

Most octopuses in the northeastern Pacific have been taken with octopus pots or boxes, and incidentally with bottom trawls (Koyama 1976; Pennington 1979). Japanese landings from the Bering Sea and northeastern Pacific have been 200–1200 t during 1977–80 (Sato and Hatanaka 1983). Washington State landings have been 15–50 t·yr^{-1} recently. The market for octopus in the northeastern Pacific is bipartite: much goes for bait for the North Pacific halibut longline fishery, but *O. dofleini* is also highly valued for food in Japan and locally in western North America. The short life span and sedentary habit of this species make it very susceptible to overfishing. Other species which are probably abundant enough to support limited fisheries in the northeastern Pacific are *O. rubescens* and *O. leioderma* (Wilson and Gorham 1982b).

Octopus conispadiceus also undertakes seasonal inshore–offshore migrations, being in deeper water during summer and shallower during winter. Eggs are laid in shallow water, and brooded by the female, who dies after they hatch.

This species is the second most frequently taken octopus in northern Japan. It is probably not overexploited, although it may be susceptible to pollution problems (Osako and Murata 1983).

Octopus macropus is important to artisanal fisheries throughout its range (Chikuni 1983; Roper et al. 1984). This species eats crustaceans, molluscs, and fishes (Roper et al. 1984).

Cistopus indicus is of significant importance throughout Asia and the Philippines (Roper et al. 1984). In Hong Kong annual landings are about 50 t (Voss and Williamson 1971).

Potential Fisheries

The possibility of expanding cephalopod fisheries on a global basis has been the subject of increasing concern in the last few years (Gulland 1971; Voss and Williamson 1971; Rathjen 1973, 1983; Tung et al. 1973; Voss 1973, 1983; Anon. 1975; Quiroz and Lopez 1979; Mesnil 1977, 1980; Wilson and Gorham 1982a; Mercer 1981; West Coast Fishery Development Foundation 1983; Caddy 1983; Roper et al. 1984). Although stock assessment techniques are poorly developed even for traditionally exploited species, estimates of potential annual cephalopod harvests range from 10 to at least 100 million t, perhaps approaching 600 million t (Gulland 1971; Anon. 1975; Peres 1980; Caddy 1983). Laevastu and Fiscus (1978) estimated that the marine ecosystem of the North Pacific consumes about 220 million t squid every year, of which perhaps 5–50 million t is harvestable by man (Gulland 1971). In the near future, most of this must come from traditional kinds of fisheries, although major strides have been made recently in the culture of cephalopods, with quasi-nektonic species cultured through the life cycle (e.g., Yang et al. 1980a,b, 1983a,b). The most encouraging possibilities are nightlight and jig fisheries on species in the family Ommastrephidae. Potential yield for each of 23 ommastrephid species and subspecies has been estimated to be at least 500 000 t (Anon. 1975; Hamabe et al. 1976a,b). Among the ommastrephids, good prospects include *Ornithoteuthis volatilis* (Japan and the south Pacific), *Nototodarus hawaiiensis* (Hawaii), *N. philippinensis* (Japan, Philippines, South China Sea, East China Sea), *Symplectoteuthis luminosa* (North Pacific), *S. oualaniensis* (Indo-Pacific), *Dosidicus gigas* (eastern Pacific), and *Ommastrephes bartrami* (cosmopolitan) (Okutani and Hatanaka 1976).

In the northeastern Pacific, a number of other species represent potential commercial fisheries: *Gonatus* spp., common in neritic to oceanic waters throughout the Subarctic Pacific (Longhurst 1969; Jefferts 1983); *Berryteuthis anonychus* (Macfarlane and Yamamoto 1974); *Onychoteuthis borealijaponica*; and possibly *Todarodes pacificus*, which may occur off British Columbia (Macfarlane and Yamamoto 1974). It is likely that fisheries for *Octopus dofleini*, *Berryteuthis magister*, *Gonatopsis borealis*, and *Loligo opalescens* can be exploited to a significantly greater extent.

In the northwestern Pacific, most cephalopod fisheries can probably support increased fishing pressure. The exceptions are fisheries around Japan for *Octopus vulgaris*, *Todarodes pacificus*, and *Ommastrephes bartrami* (Okutani 1977; Osako and Murata 1983).

Rational exploitation of cephalopod stocks in the North Pacific will require better estimates of stock size, reproductive potential, predator–prey and competitive interactions, and recruitment relations, as well as development of appropriate fishing and processing technologies and marketing strategies.

The ability to make accurate estimates of stock size is fundamental to any sort of management scheme, and would probably allow realization of increased yields. Our knowledge of the reproductive biology is near zero for most species. Such information as fecundity, age at first spawning, post-reproductive senility (or lack thereof), longevity, spawning location, temperature requirements for hatching, and the ecology of hatchlings are necessary management data, but are known, even partially, for very few species.

Population dynamics of most commercially important cephalopods are significantly different from those of exploited fish populations. Cephalopods are primarily annual species, may function at more than one trophic level (with significant cannibalism in some species), and exhibit very high production relative to their standing stock (e.g., Ehrhardt et al. 1983b). The two groups may interact, however. Significant evidence has accumulated that overexploitation of fish populations may allow competitive release of cephalopod populations (Fields 1965; Saila and Parrish 1972; Laevastu, in Mercer 1981; Caddy 1983).

Cephalopods are of major importance in the diets of many fishes and marine mammals. Any exploitation scheme must thus consider effects on commercially and aesthetically important species.

Gear development could greatly affect the course of cephalopod fishery development in the North Pacific. To wit, use of drift gillnets since 1978 has allowed exploitation of major resources of squid in the open waters of the North Pacific. Similar order of magnitude jumps in landings could be effected by development and deployment of gear to capture non-schooling and deeper-living oceanic stocks. In a like manner, advances in processing technology might allow use of currently undesirable species, such as *Rossia pacifica* and *Moroteuthis robusta*, both of which represent major stocks on the shelf and slope around the North Pacific rim.

Marketing of cephalopods, which are often regarded as strange and undesirable oddities by Western consumers, remains a major obstacle. The Orient has historically been, and remains, the primary market. Recent developments, however, indicate that this is slowly changing. Promotion of *Dosidicus gigas* (Blake 1982) in western markets is a notable example of latent potential.

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A Perspective on Invertebrate Fisheries Management — the British Columbia Experience

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The recent history of invertebrate fisheries management is discussed in the context of problems addressing both fisheries management in general and those aspects unique to invertebrates. Areas of interaction between researchers and managers are identified and discussed, and contributions of researchers in general are analyzed in relation to traditional provision and use of biological advice. Management histories of four British Columbian fisheries (Dungeness crab, geoduck, abalone and prawn) are evaluated and strengths and problem areas discussed.

Individual invertebrate fisheries in British Columbia will always likely be minor relative to the region's major fisheries, notably salmon, and will never warrant investments in data collection, monitoring and research required for active management. Management should be simple, using common sense and elementary, easily enforceable regulations such as minimum size limits. Restrictive regulations such as quotas or fishery closures may be necessary at somewhat arbitrary levels or dates to control effort or landings until species population dynamics are better understood.

It is impractical to develop a common management approach for all invertebrate fisheries because of diversity in both species biology and fishery type. In those fisheries where most, if not all, animals are lethally damaged through capture, management emphasis should be on trying to exploit a predetermined percentage of the available biomass. However, in size-selective fisheries where individuals can be released with minimal physical damage, management should focus on optimizing yield and/or egg production from whatever level of recruitment occurs, rather than trying to control future recruitment and achieve stability in landings. Objectives of management, and any assessment of management performance, should reflect the suggested general inability of man to influence recruitment magnitude for most invertebrates within historic ranges of population abundance. Exceptions to this in British Columbia may be abalone, with their relatively short larval dispersal period, and protandric hermaphroditic shrimp, where the fishery tends to focus on females.

L'article traite de l'histoire récente de la gestion des pêches des invertébrés, en ce qui a trait aux problèmes relatifs à la gestion des pêches en général et aux aspects particuliers aux invertébrés. Il identifie et traite les domaines d'interaction entre les chercheurs et les gestionnaires et analyse les contributions de l'ensemble des chercheurs en ce qui a trait à la prestation et à l'utilisation traditionnelles des conseils d'ordre biologique.

L'historique de la gestion de quatre pêches de la Colombie-Britannique (crabe dormeur, panopea du Pacifique, ormeau pie et crevette tachée) y est analysée, et on y traite des points forts et des problèmes.

Les différentes pêches des invertébrés de la Colombie-Britannique demeureront probablement toujours secondaires par rapport aux grandes pêches de la région, notamment le saumon, et ne justifieront jamais des investissements en collecte des données, contrôle et recherche nécessaires à une gestion active. Leur gestion doit être simple, basée sur le bon sens et des règlements élémentaires facilement applicables, tels que des limites minimales de grosseur. Des règlements restrictifs, comme la fixation arbitraire du niveau des contingents et des dates de fermeture de la pêche, pourraient s'avérer nécessaires pour contrôler les efforts de pêches ou le volume des débarquements jusqu'à ce que l'on ait une meilleure connaissance de la dynamique des populations des différentes espèces.

Il est impossible d'établir une méthode commune de gestion pour toutes les pêches des invertébrés, en raison de la diversité de la biologie des espèces et des types de pêche pratiqués. Dans le cas des pêches où la capture entraîne la mort de la plupart, sinon la totalité, des animaux, la gestion devrait surtout porter sur l'exploitation d'un pourcentage prédéterminé de la biomasse disponible. Cependant, dans le cas des pêches à grosseur déterminée, où les prises peuvent être relâchées avec un minimum de dommages physiques, la gestion devrait se concentrer sur l'optimisation du rendement et/ou de la production des œufs à partir d'un niveau de recrutement donné, plutôt que d'essayer de contrôler le recrutement futur et de stabiliser le volume des débarquements. Les objectifs de la gestion, et toute évaluation du rendement de la gestion, devraient tenir compte de l'apparente incapacité générale de l'homme jusqu'à maintenant à influer sur le volume du recrutement de la plupart des invertébrés aux différents niveaux d'abondance des populations, à l'exception peut-être, en Colombie-Britannique, de l'ormeau pie, en raison de sa période de dispersion larvaire relativement courte, et de la crevette hermaphrodite protandrique, lorsque la pêche tend à se concentrer sur les femelles.

Introduction

Efforts made by governments over the last few decades to manage fisheries have generated an extensive literature on the status of many fishery resources. It should be possible to evaluate and learn from consequences of earlier management actions. Since both resources and their exploitation are dynamic, study of the progression of resources from an unexploited state to a fully exploited, or occasionally overexploited, state should result in coincident refinement in goals or objectives of management. In any evaluation of successes and failures of management, and the role which biological advice has played, it is important to try to establish what the rationale and objectives of management were at the time decisions were made.

In this paper, evolution of management rationale and alternative approaches for management are discussed for four British Columbian invertebrate fisheries. Biological advice and how it has been utilized as both resource status and exploitation level have varied are considered. Relevant conclusions derived from management of other fisheries, where such concerns have been more extensively considered (e.g. FAO 1980), are presented. This demonstrates other perspectives and the fact that present concerns are not always unique and have been documented previously in the published literature. The difficulty in incorporating experiences from other jurisdictions into a regional management process is considered.

Science versus Management

A number of recent studies (Garrod 1975; Rothschild 1983; FAO 1980) attempt to explain why the full benefits of earlier resource management efforts have not been achieved, and why the seemingly simple objective of extracting full benefits from a closely regulated fishery is so difficult to realize. In many fisheries, different interest groups have pursued conflicting objectives, resulting in either no decisions being made or imposition of a lower-benefit compromise by managers (e.g. sea scallop: Pierce 1983; abalone: Cicin-Sain et al. 1977). Management is the process of making decisions, based presumably on relevant concerns (biological, social and economic), and it is often as important simply to make a decision in time as it is to make precisely the right one. In contrast, science should present evaluations of specific actions or the potential consequences of future ones, and so facilitate the making of rational decisions.

The evolution of fisheries management philosophy from 1850 to 1975 has been summarized in detail (e.g. Neilsen 1976; Larkin 1977). The concept of inexhaustible ocean resources requiring minimal management gave way near the turn of the century to the objective of maximizing sustained physical yield from a resource, which in turn evolved in recent years to recognition of other relevant, non-biological objectives. This relatively recent development arose from the general failure of biologically oriented advice, particularly maximum sustainable yield (MSY), to produce satisfactory long-term benefits from fisheries resources. The alternate view of the importance of maximizing economic aspects of a fishery, embodied in the concept of maximum economic yield (MEY), is also unsatisfactory (Garrod 1975). Though both MSY and MEY are attractive theoretically, both have proven difficult to define in a practical sense. Uncertainty about both multispecies and stock: recruitment relationships and the common property nature of the resource has compromised use of MSY (Healey 1984; Larkin 1977). With allocation of a resource to a group (e.g. fishermen) and little assessment of yields derived from additional units of effort, additional effort will be expended as long as profits are being made, either by increased fishing per fishermen or by more fishermen. This competition for available catch, with its resulting conflicts, ultimately leads to curtailment of economic benefits. Similarly, the comparable complexity of economic factors has made use of a MEY equally inappropriate.

The management concept that has gained general acceptance in recent years embodies biological, economic and social perspectives, with a flexible, pragmatic approach accommodating any goal (Roedel 1975). In Canada, fisheries resources are generally considered public property and it is the responsibility of government to control their use (Healey 1984). The concept of optimum sustainable yield (OSY) separates fisheries management from control by any specific discipline, biological or otherwise. Whatever society, not fisheries science alone, perceives as best become acceptable objectives, and this underlies the one absolute goal of fisheries management today: development and presentation of a broad range of actual and potential opportunities.

It should be noted that this is broader than the definition of optimum sustainable yield described by the International Council for the Exploration of the Sea, or ICES (Anon. 1977), which includes adjustment of the simple MSY-concept to address other biological concerns. In most fisheries management, scientific advice only relates to biological implications, with both the "experience" of managers and the views of interest groups providing the basis for socio-economic decisions. Documentation of biological advice alone, however, still tends to give fisheries management an expectation of precision beyond that which can reasonably be expected even after lengthy study. Extensive development of models and analytical procedures in recent years has further enhanced this perception, and has made it even more difficult for managers and fishermen, who often have little sophisticated analytical experience, to understand fully advice being provided. Since models by definition are simplification of a complex reality, the exact behaviour of the system being studied is unpredictable to a significant degree. The problem of how to manage optimally is not related specifically to inadequacy of fishery policy or implementation, but is complicated by the fact that fisheries are now intimately intertwined in the overall complex of controversial issues (e.g. unemployment, pollution, urban development, etc.) with which modern societies are attempting to deal. Unanticipated events further challenge the ability of fisheries science to be predictive and useful in a long-range planning capacity, and this can erode the confidence of managers in knowledge scientists claim to have of a specific stock's population dynamics. No easy or simple solutions are likely to be found.

Rationale For Management

How effective is present-day, Pacific invertebrate fishery management? Have management rationales behind present regional regulations been clearly defined, and are they based on OSY philosophy or on older dogma whose merits have been shown to be tarnished? In attempting to evaluate this for Pacific species, the major problem of the general scarcity of published information about the management of Pacific invertebrates is exposed.

In the Pacific, in contrast to the Atlantic, there are no government-supported international fora for discussion and documentation of scientific advice and management decisions for invertebrates. This reflects the overwhelming importance of salmon in the region, which has, along with groundfish, its own international forum, the International North Pacific Fisheries Commission (INPFC), but it is also based on the generally near-shore, national nature of traditional invertebrate fisheries. In the eastern Pacific, this is largely because of narrow continental shelves, with the main exception being the wide continental shelf of the Bering Sea with its substantial king and tanner crab stocks. In the absence of major historic, international-water invertebrate fisheries, management has been the prerogative of individual nation states, and no international commissions, such as the North East Atlantic Fishery Commission (NEAFC), obtaining its advice from an independent scientific body, ICES, or the International Commission for Northwest Atlantic Fisheries (ICNAF), now the Northwest Atlantic Fisheries Organization (NAFO), have been developed to include Pacific invertebrates. There is a shellfish subcommittee in the Pacific Marine Fisheries Commission (PMFC) of the United States which deals with interstate issues (e.g. crustacean handling mortality, transport of animals between geographic areas), but this forum is not international nor as publication-oriented as are the above Atlantic examples. As a result, little scientific incentive to publish fisheries stock assessment and management-related manuscripts on a real-time basis has been generated, since most scientific journals do not accept such parochial manuscripts. Management advice and concerns have either not been published or have been published in an *ad hoc* manner in scattered, relatively unavailable secondary publications (e.g. state and provincial publications and federal data and manuscript reports of limited distribution).

The relative lack of documentation of events has meant little extensive review in analysing the state of resources and evaluating the effects of different management actions. Data collection and compilation methodology is often difficult to determine and in general, this has made it difficult to compare experiences between regions in a meaningful manner. For the purpose of this paper, it has been necessary to contact managers personally to determine most management rationale and events behind past and present regulations. As a result, non-Canadian fisheries could not be described here easily, and so only select, British Columbian fisheries are considered in later detailed analyses.

Management rationale can be classified in many ways but for the purpose of this discussion, regulations have been categorized by both the type of management activity (Table 1) involved (FAO 1980) and by the management concern (Table 2) being addressed (Miller 1976):

A. MANAGEMENT ACTIVITY

FAO (1980) has categorized data required for management into four categories according to ultimate user and type of management activity involved. I have utilized their terminology to further categorize management rationale:

1) *Immediate Management*: The objective is to achieve maximum benefit in the short-term from resource utilization. This includes exploiting stocks on the basis of current stock status and distribution, using such tools as quotas and minimum size limits. It meets real-time social and economic concerns, and involves allocation between different users and the maximizing of product quality by control of fishing techniques.

2) *Preventive Management*: The objective is to optimize resource utilization over the long-term. Areas of future concern are identified, and procedures are effected to maintain stability in achievement of desired

TABLE 1. The perceived rationale behind British Columbian management regulations for invertebrates, classified by management activity.

1. IMMEDIATE
- **area and seasonal quotas** — abalone, geoduck, shrimp (trawl), euphausiids, sea urchin
- **minimum size limit** — abalone, intertidal clams, crab, sea urchin
- **license requirement** — mussels, octopus, squid, crab, shrimp (trap), prawn, euphausiids, sea urchin
- **area and seasonal closures** — octopus, crab, shrimp (trap), prawn, euphausiids, sea urchin

2. PREVENTIVE
- **gear restriction** — all exploited species
- **limited entry** — abalone, geoduck, shrimp (trawl), horse clams (subtidal)
- **closed areas** — shrimp (trawl and trap), intertidal molluscs, horse clams (subtidal)

3. REMEDIAL
- **None**

4. RESEARCH
- **fishing log completion** — abalone, geoduck, shrimp (trawl and trap), goose barnacles, octopus, euphausiids, sea cucumber, sea urchin
- **closed/open areas** — abalone, geoduck, sea cucumber
- **experimental permits** — shrimp (trawl)

benefits. Examples include minimization of prerecruit mortality by protection of nursery grounds and gear restriction and maintenance of the economic viability of individual fishery units by effort restriction.

3) *Remedial Management*: The main goal is to improve the present level of achieved benefits, it being implicitly recognized that the situation permits managers to exert control either over the events which decrease return or to enhance return by the introduction of new, external factors. Examples include the rebuilding of devastated stocks to a level capable of supporting a fishery by area closures or wild stock enhancement with cultured animals, and the reduction of excessive fishing effort by license buy-back policies.

4) *Research Management*: The objective is to obtain data required for development of optimum management by permitting small-scale, controlled exploitation. This is frequently the first step in the development of a new fishery, and an example would be an effort-restricted fishery with the requirement for fishermen to provide detailed documentation of catch and expended effort. This approach also includes intentional perturbation of the system in a non-optimal manner, and the subsequent monitoring of response so as to gain a better understanding of system dynamics.

B. MANAGEMENT CONCERN

1) *Conservation*: to maximize physical yield and minimize resource wastage during the fishing process.

2) *Allocation*: to partition annual catch among participants fishing the same species, either by season, area or gear type.

3) *Stability of Return*: to even out economic return between above- and below-average years of resource abundance.

4) *Conflict Over Grounds or Resource*: to resolve competition between fishermen for fishing grounds (e.g. trawlers versus fixed trap fishermen) or different fishery resources (e.g. incidental scallop dragger damage of crustaceans). Miller (1976) includes sport-commercial conflicts here but depending on their nature, these could be considered under "allocation".

5) *Processing Economics*: to limit landings to a size and quality that can be processed at a profit acceptable to processors.

6) *Social Factors*: to restrict landings of designated type to specific user groups (e.g. native peoples) or to prevent fishing in environmentally unique areas (e.g. national parks, ecological reserves). This category was not considered by Miller (1976).

7) *Administration*: to facilitate documentation of the fishery and its performance (e.g. licencing and registration of vessels and gear and collection of fishery data).

It is evident that for most species, present regulations may have a number of objectives and that their relative effectiveness in each is uncertain. Indeed, as discussed by Rothschild (1983), most fisheries today have a mix of conventional objectives which regularly change in response to continually changing biological and economic factors. Performance is difficult to quantify and operationally is often subjectively evaluated by frequency of expressed concern from interest groups.

TABLE 2. The perceived rationale behind British Columbian management regulations for invertebrates, classified by management concern.

1. CONSERVATION
   — **area quotas and seasonal closure** — abalone, geoduck, shrimp (trawl), sea urchin
   — **gear restriction** — all exploited species

2. ALLOCATION
   — **vessel quota** — abalone

3. STABILITY OF RETURN
   — **minimum size limit** — abalone, intertidal clams, crabs, sea urchin
   — **limited entry** — abalone, geoduck, horse clams (subtidal), shrimp (trawl)
   — **area quota** — geoduck
   — **seasonal closure** — prawn, shrimp (trap)

4. CONFLICT OVER GROUNDS OR RESOURCE
   — **area closures** — shrimp (trawl and trap), euphausiids
   — **quotas** — euphausiids
   — **seasonal closures** — euphausiids

5. PROCESSING ECONOMICS
   — **season closures** — crabs, sea urchin

6. SOCIAL FACTORS
   — **closed areas** — abalone, intertidal clams, octopus, crabs
   — **human health closures** — horse clams (subtidal), intertidal molluscs, goose barnacles

7. ADMINISTRATION
   — **closed areas** — abalone
   — **fishing log completion** — abalone, geoduck, shrimp (trawl and trap), octopus, goose barnacles, euphausiids, sea cucumber, sea urchin
   — **research study areas** — geoduck, shrimp (trawl), sea cucumber
   — **license requirement** — mussels, octopus, squid, crabs, goose barnacles, prawn, euphausiids, sea cucumber, sea urchin, abalone, geoduck, horse clams (subtidal), shrimp (trawl)

Management objectives have been well documented for some exploited invertebrate stocks, e.g. Western Australian prawn (Bowen and Hancock 1982), rock lobster (Hancock 1980), stone crab (Anon. 1978), and deficiencies have been identified for others, e.g. clams (McHugh 1978). In general, there has been limited definition in the literature of management objectives for exploited, eastern Pacific fishery resources. A broad national exploitations policy for Canadian commercial fisheries has been described (Anon. 1976) but while considerable attention is currently being directed towards evaluating management policy at the regional level, recent regional policy in British Columbia has been published only in booklets of fisheries regulations (e.g. Anon. 1983, 1984) given annually to fishermen. The specific objectives of management on a fishery basis are generally unavailable. Pearce (1982) discussed general policy objectives but the extent to which his recommendations have been accepted is still not clear.

In British Columbia, the most recent statement (Anon. 1984) is:

> "The prime objectives . . . are to manage, conserve, and enhance the tidal and anadromous fish stocks of British Columbia and the Yukon Territory for the greatest possible benefit from the renewable fishery resource."

The Alaskan state management objective (Anon. 1983) for king crab is more specific, and states:

> "The policy of the Board of Fisheries is to manage the Alaska king crab fishery in a manner that establishes stability and eliminates, as much as possible, extreme fluctuations in annual harvest that have at times characterized the fishery. The Board recognizes that this policy will not maximize physical yield because maximum physical yield will not necessarily produce the long-term optimum economic yield."

In 1983, however, this was the only Alaskan resource for which management objectives were published, although management strategies were provided for Kachemak Bay shrimp. Other American states may have published management plans for a few, selected species but in general, clear statements of management objectives are difficult to obtain for most species.

One of the simplest definitions of an objective of present-day fisheries management is that given by Bowen and Hancock (1982) for the limited-entry prawn fisheries of Western Australia, which recognizes the possibility of recruitment overfishing as well as the importance of economic factors:

> "the maintenance of the resource at a level approaching the maximum sustainable yield, while giving proper attention to the economic viability of the fishing units with a view to maintaining a profitable industry."

ICES (Anon. 1977) suggested that the main biological objective should be the MSY-concept with conditional qualifications. These should primarily address the stock:recruitment relationship and exploitation pattern, with secondary objectives being to maintain size of the exploitable stock at a sufficiently high level to partially dampen fluctuations caused by year to year variations in recruitment and to avoid unnecessary harvesting costs. This objective, however, was established for finfish and its applicability to invertebrates needs detailed consideration. For example, the relatively high fecundities of some species (e.g. bivalves) raises questions as to the usefulness of considering stock:recruitment relationships, although for some of the larger crustaceans, such an approach may have more merit.

What is required to evaluate management success is a restructuring of general objectives into identifiable components which can be more readily quantified and assessed. Criteria for socio-economic parameters could be fishermen's incomes, the number of active participants (fishermen, fish plant workers, etc.) or the resources required for effective fisheries management. Biological criteria could include maintaining a specified minimum stock size or population size frequency structure over a specified time period, or maintaining specified harvested species proportions with different relative population sizes in a multispecies fishery. Standards to be achieved in criteria such as the above would provide a benchmark of performance in any evaluation process.

Failure to define and document clear objectives not only makes evaluation of alternate management approaches difficult but may also impede consideration of viable alternative approaches. The problem of developing appropriate objectives for management of Canadian east coast fisheries has been studied in detail (Inst. Environ. Studies 1977), but transmittal of relevant considerations to working-level managers in most regions appears to have largely failed. In British Columbia at least, much remains to be addressed.

Management Strategy

It is immediately obvious that with management objectives broadly defined, interaction between management strategies designed for different components and goals becomes complex. Studies (e.g. Inst. Environ. Studies 1977) describing methods of interpreting alternatives in the context of implied objectives are relevant to managers, but because the backgrounds of many researchers and managers does not include relevant theory, they frequently are unaware of available options. As a result, much of fisheries management, as indicated by Pearce (1982) in his evaluation of British Columbian fisheries, has an *ad hoc* appearance with little demonstrated evidence of overall planning.

The common property problem referred to earlier and the reduction of fishing effort to optimal levels has been dealt with traditionally through both restrictive (e.g. catch or effort quotas) and economic restructuring (e.g. taxation) methods. Intermediate techniques such as the auction of licences have also been advocated |e.g. by Pearce (1982) for salmon|, and in Washington State, fishing rights to specific areas for geoducks (*Panope abrupta*) are routinely auctioned (L. Goodwin, pers. comm.; Sloan 1985). Most present management practices in invertebrate fisheries are based on restriction and involve techniques such as season and area closures, gear and size restrictions, catch quotas and limited entry. Although problems exist, restrictive management appears most acceptable at this time to both fishermen and society, perhaps because it is the one approach they are most familiar with historically.

Hancock (1979) described five types of management strategies: no regulation; three alternative restrictive management approaches (specific regulation, effort limitation and catch quotas); and aquaculture management, perhaps better described as enhancement management. He also considered management strategy and the evolution of research programs in terms of fishery state: undeveloped, developing and fully exploited. Among invertebrates, there appears to be no special advantage to any one management strategy on the basis of systematic grouping (e.g. phylum, class or family) or ecology (e.g. nearshore vs offshore, temperate vs tropical, etc.) except insofar as they relate to ease of collection and type of data available for management purposes, and to the practicality of enforcement. Fishing strategy (e.g. gear type) may effect management more directly since some approaches are not very selective and may lethally damage most, if not all, individuals caught.

Investigative biologists have traditionally been the group which has decided what, where, for how long and in what quantity data should be collected, and since appropriateness of management strategy is greatly influenced by available objective information, researchers have had a significant role in the determination of management approach. How researchers have perceived management and its needs is thus very relevant, particularly since many career managers have frequently had an earlier "research" background.

Choice of management strategy has also been influenced by how long ago and for what reasons a resource first becomes managed. In contrast to finfish, many present invertebrate fisheries were initially traditional, subsistence fisheries, and being mostly inshore, they were readily exploited by local populations. Landings were widely distributed geographically, and so passive management strategies evolved which reflected moderate exploitation and limited enforcement and research resources. These typically had little direct effect on annual yields or number of fishermen.

Management of such fisheries often first involved imposition of a minimum size limit for both conservation and economic reasons and to provide objective criteria for enforcement. This form of regulation is particularly effective with invertebrates since in most such fisheries, animals are readily handled individually and in a manner which causes little mortality, if any, after release of sublegal size individuals. Generally, little effort historically was made to define stocks accurately and to document stock status. Exploitation level and expectations have changed with time, however, and new improved handling and transportation procedures have been developed. Many invertebrates are now considered luxury products, and in recent years, fishing effort has dramatically increased in many long-term, historically stable, fisheries, raising concern about future effects of current exploitation levels.

In recent years, managers have had three options: (1) do nothing [e.g. most intertidal clam fisheries, with a regional exception being razor clams (*Silqua patula*) in Washington]; (2) impose additional restrictive measures such as area and seasonal closures, limited entry and so on, or attempt active management through use of annual quotas (e.g. many crustacean fisheries); or (3) develop a whole new fishery approach, such as aquaculture (e.g. oysters and mussels) or experimental fisheries management. When additional fishery restrictions are imposed, components (e.g. fishermen) affected can be expected to seek to optimize activities in the context of their own objectives (e.g. making a profit) in response to constraints imposed by management. Resistance to change is an almost universal property of self-regulating systems, and it can be expected that components will respond in a way which tries to mitigate effects of external perturbations (Inst. Environ. Studies 1977). Responses can be within a single fishery (e.g. the accumulation of licenses under the control of one individual) or involve a number of fisheries, such as establishment of a multispecies fishery situation. This combined adaptation and resistance to change appears often not to have been anticipated by managers, with actual results perhaps quite different from those initially desired or anticipated. This in turn often leads to new restrictions, with the end result that management becomes more reactive then anticipatory. The ability to assess satisfactorily the performance of individual management actions becomes lost in the web of resulting regulations. Unfortunately, this is the direction in which management of many invertebrate fisheries is heading today.

An alternate scenario is demonstrated by those fisheries which were initiated in the past decade or are in the process of developing now. In Canada at least, the infrastructure currently exists to impose rigorous management for newly developing fisheries. Conservative approaches such as the step-wise development advocated by Gulland (1972) would seem appropriate. Unfortunately, whereas this may be possible theoretically, the rapid momentum generated by the perceived potential of significant profits seems in some cases at least (e.g. abalone) to have resulted in the same uncertainty as to future direction that exists in management of many traditional fisheries. While a comprehensive regulation "package" may have been initially envisaged, rapid overexploitation of the fishery occurred and the only obvious conclusion to be drawn in hindsight was that not enough initial caution was applied.

Once a fishery is established, fishery restriction without extensive supporting evidence is often difficult to initiate and even if established, problems often arise. Catch quotas are often difficult to enforce, since invertebrate landings are often wide-spread geographically and relatively small, and this can lead to serious underreporting of actual landings. From a restrictive management perspective, it has been stated that theoretically, effort quotas, although perhaps also difficult to effect, are less destabilizing than comparable catch quotas (Inst. Environ. Studies 1977; Gulland 1983). With a catch quota, the amount of effort expended generally increases when a stock declines. Periodic declines in stock abundance can be expected, because of both natural fluctuations induced by environmental change and imbalances within the management system. Unless the management process can respond quickly in crisis situations by adjusting harvest quotas to conservative levels (e.g. the recent closure of the Kodiak king crab fishery), dependence on catch quotas as a management tool should be treated with particular caution.

Use of Biological Advice

Provision of soundly based biological advice to managers fulfills two prime functions: (1) it describes the state of the resource and indicates concerns related to conservation of the resource, and (2) by estimating the maximum physical yield which can be derived, provides managers with a benchmark with which to evaluate possible effects arising from other management considerations. The extent to which biological advice is actually used by managers depends on:

1) its nature,
2) its timeliness,
3) its accuracy and precision.

To be effective, scientists have to understand the real needs of management and produce analyses which address these concerns. For example, if a fishery is progressing well, and resource status appears stable, preventive management may be a manager's greatest concern and information relating to the likely occurrence of disturbances to the system may be most desired. Extensive effort applied by scientists to document fishery performance and resource state may be of value in completing a long-term data base but provides managers with little information of value in the short term.

In considering the use of data in relation to research and management modelling (Inst. Environ. Studies 1977), it has been stated that most models are built for the understanding of the model-builder; biological models of fisheries are primarily designed to study the interactions of interesting biological parameters. There has been a lack of management models designed to address management concerns. Research models tend to maximize both quantity and precision of information generated, and hence approaches which might yield poorer-quality output data, such as stochastic models, seem less useful. Information required by management, however, often merits consideration of such elements and while precision is always important, model output must be useful to the client. Conflict between scientists who give managers answers to questions of lesser relevance, and managers whose questions may appear vague and parochial to scientists, is not infrequent. Research models often try to indicate how to respond to change, anticipated or otherwise. Walters (1975) argues that for most researchers, a radical shift in our basic way of thinking about system decision problems is required. Rather than imposing a policy on a simulated system and evaluating system consequences if a policy fails, scientists should rather ask, or at least include, questions about decision consequences of policy failure.

Need of managers for timely advice has been well documented (Inst. Environ. Studies 1977; FAO 1979): management requires decisions to be made and while complete information is preferred, its absence may not defer a decision. Management typically involves both long-range and short-term goals, and time frames for submission of advice relevant to achieving these objectives often differ. Long-range planning permits more careful thought and study and should include consideration of all factors affecting any given process. Many management problems involve a compromise between long-term goals and the immediate needs of the present, and for these short-term events opportunity for detailed deliberation is often limited. This is where contingency planning proves particularly useful.

Fishery Examples

To investigate how biological advice has been used in management of select British Columbian invertebrate fisheries in recent years, case histories of four major fisheries are described in detail: one long-term, relatively stable fishery (Dungeness crab), two short-terms stabilizing fisheries (geoduck and abalone), and one rapidly expanding fishery (prawn).

CASE HISTORY #1: DUNGENESS CRAB

Biology and Fishery

Dungeness crab (*Cancer magister*) is the main commercial crab currently exploited in British Columbia. Males are predominantly harvested and generally are fished in waters of less than 30 m depth. Commercial fishing (Fig. 1) has been conducted since the late 1800's and by 1940, more than 100 licensed fishermen were landing 450 t annually. In 1950, the fishery expanded rapidly in northern British Columbia when American fishermen with improved gear entered the Hecate Strait fishery. Canadian fishermen adopted similar gear and in 1967, landings peaked at 2405 t. Subsequently, landings have declined, particularly in Hecate Strait (Jamieson 1985; Noakes 1986), and although there has been some increase in recent years, exploitation is intense and CPUE remains relatively low. Landings in the south have remained more stable, but within each subfishery,

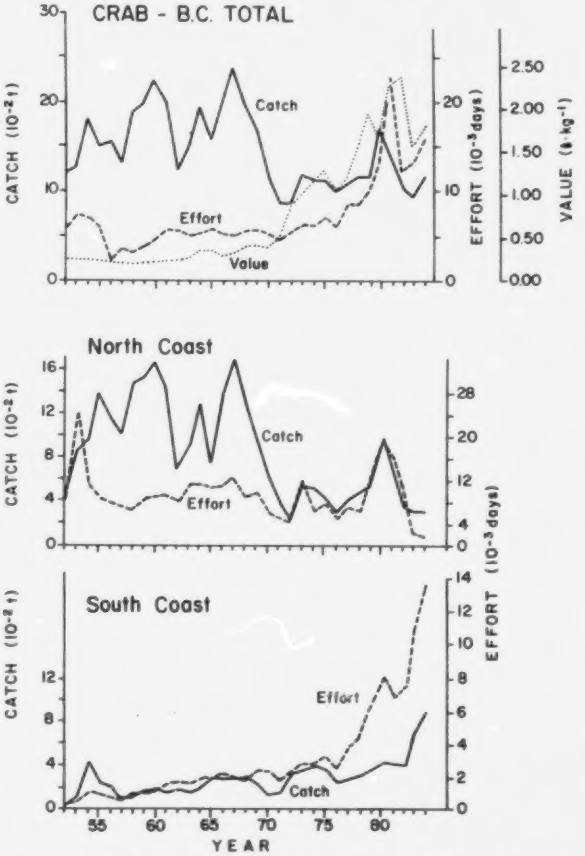

FIG. 1. Annual catch, effort, and unit price for the British Columbia Dungeness crab fishery. The North Coast is that geographical area north of Cape Caution. Source: Annual B.C. catch statistics, Statistics Division, Field Services Branch.

fluctuations have still been considerable (Jamieson 1985). In 1984, reported landings were 1155 t with a value of $4.6 million.

Spatial distribution and abundance are poorly documented, as are factors affecting recruitment. All stocks are exploited fully and little expansion of the fishery is predicted (Bernard 1982).

Chronology of Biological Advice and Management Decisions

There has been relatively little biological advice given to and requested by managers since the early 1900s with respect to how the crab fishery should be regulated and managed. Some local seasonal closures have been established to address area-specific concerns (e.g. soft-shell fishing) but these have not been applied coastwide. The minimum legal size of 165 mm (spine to spine width), probably established in the 1910's, was presumably set so that male crabs would be mature for 2–3 years before they recruited to the fishery. Relatively few females reach this size and so they are seldom exploited.

Assessment of Management

In general, there has been a relative absence of management concern with crab, and this has been reflected by limited research in recent years. This results from few perceived problems and a general acceptance of the present management approach, but it may also reflect the nature of the fishery itself. Crab fishing is part of a multispecies fishery, with 40% of the approximately 350 fishermen who participate each year dropping out and being replaced by others. The number of fishermen participating annually has been relatively constant, but only 5% of the 948 participants over the past 6 years have fished for all 6 years (Jamieson 1985). Only a few crab vessels roam the entire coast and most fishermen restrict their fishing to specific geographic areas. Crab fishermen as a group have no organization to lobby their views on crab, although many crab fishermen belong to organizations which express their collective views on the exploitation of the region's main fishery resources, notably salmon. In a choice situation, priority has been directed towards those fisheries which provide most income over the long term, and which unlike crab, seem particularly sensitive to man-induced perturbation.

There is little evidence that the Canadian crab fishery, with current regulations, has had any effect on the magnitude of crab recruitment in British Columbia. Whether or not the crab resource has been exploited optimally, a general regional objective of management, has not been investigated, although some limited studies have recently been initiated which will partially address this question.

CASE HISTORY #2: GEODUCK

Biology and Fishery

Geoducks (*Panope abrupta*) are large, subtidal bivalves, widely distributed in the eastern Pacific from Washington to Alaska. They are long-lived (140+ yr) and harvested animals average over 1 kg in weight (Harbo et al. 1983) and may be found at densities up to about 40 m^{-2} from the intertidal zone to at least 110 m depth. However, only animals <20 m depth are exploited due to diving time restriction associated with deeper diving. They bury to 80 cm and when dug up, generally cannot rebury themselves. Growth is rapid only for the first 8–10 yr and the natural mortality rate of adults is low ($M<0.02$: Breen and Shields 1983). They mature at between 4–7 yr of age (Anderson 1971; Sloan and Robinson, in press). Exploited populations typically range from about 30 to 50 yr in age (Harbo et al. 1983). There is some evidence (Goodwin 1984) that in unfished locations, juvenile geoducks are most abundant in association with adult geoducks, raising the concern that fishing could have a potential adverse effect on future recruitment.

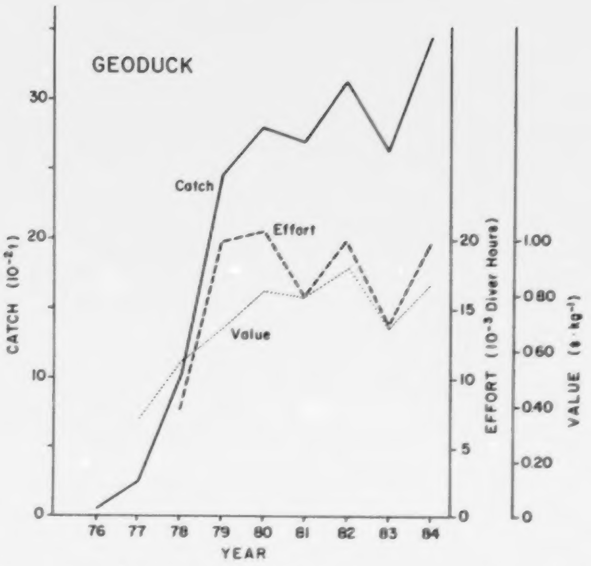

FIG. 2. Annual catch, effort and unit price for the British Columbia geoduck fishery. Source: Annual B.C. catch statistics, Statistics Division, Field Services Branch.

The current fishery (Fig. 2) in British Columbia began in 1976 and now involves 55 licensed vessels. In 1984, the landed catch was 3483 t with a value of $2.9 million, and it is anticipated that landings will be stable for the foreseeable future.

Chronology of Biological Advice and Management Decisions

(1976–1980: Harbo and Peacock 1983; 1981–1984: Harbo et al. 1986)

1976: Seven permits granting exclusive harvesting rights by area were issued for the Strait of Georgia. Americans trained Canadian fishermen. Five operators actually fished.

1977: A survey of abundance and distribution was carried out by Marine Resources Branch (MRB), Provincial Ministry of Environment, for Queen

Charlotte, Johnstone and Georgia Straits (east coast of Vancouver Island). This and following surveys were initially intended only to establish the range of commercial geoduck concentrations, but in the absence of better data, have subsequently been used to estimate standing biomass. Permits were issued until July 1, after which time licenses were required. Thirty licenses were issued, with 14 reporting landings. There were no season closures or quotas, and Americans could provide only limited training. A research area closed to commercial fishing was established in Barkley Sound.

1978: Additional surveys were undertaken by MRB in selected locations in the Strait of Georgia and west coast of Vancouver Island. Fifty-four licenses were issued, with 27 reporting landings. Goodwin (1978) reported results of American resource surveys in Puget Sound from 1967 to March 1977, with a conservative biomass estimate of 130 000 t, spread over 13 678 ha.

1979: 1977 MRB survey results were published (Cox and Charman 1979). 1978 MRB data was analyzed but it has never been published. 101 licenses were issued, and concern was now expressed by managers that MSY was being exceeded. A moratorium on licenses was imposed on June 13; managers announced that a minimum vessel landing of 13.6 t would be required for a 1980 licence. Seventy-two license holders landed geoducks. A coast wide quota of 3629 t |1588 t (north coast, i.e. north of Cape Caution); 2041 t south coast| was established after managers evaluated patterns of fishing effort, landings, surveys and expectations of stock size. Selected areas were closed on September 29 because of heavy exploitation.

1980: A joint survey of selected south coast areas was carried out by MRB and the federal Department of Fisheries and Oceans (DFO) — results were analyzed but never published. The south coast quota was increased to 2269 t, while the north coast quota remained the same. The south coast was divided into 8 management units, each with its own quota. First exploitation in the north involved 7 vessels; an additional license was required. Ninety-five licenses were issued overall, with 63 license holders reporting landings. First estimates of growth, mortality and recruitment rates were obtained (P. Breen, unpubl. data). Yield modelling (P. Breen, unpubl. data) carried out with these parameter estimates formed the basis for the present quota — 0.75–2% of the virgin biomass, but a value for this biomass was never specified.

1981: Licenses were issued only to fishermen who had landings greater than 13.6 t in each of 1978 and 1979; 52 licenses were issued, three licenses awaited new vessels, and a few fishermen appealed. Quotas were decreased to 1814 t in the south, 907 t in the north. Field studies were initiated to obtain better estimates of mortality, recruitment and growth rates by detailed sample collection at five sites. All harvested geoduck were required to be processed. Prior to 1981, geoducks with dark meat (0–75% of total population, depending on fishery location) could be discarded and were not included in official statistics. Additional modelling to evaluate sustainable yields at an equilibrium biomass equal to half the virgin biomass suggested no modification of earlier established harvest levels was required (P. Breen, unpubl. data).

1982: Total exploited area to date in B.C. was estimated to be 9993 ha (R. Harbo, pers. comm.). The recommended quota was held constant for the north and increased to 2041 t in the south. The first commercial catch samples were collected. A summary of Breen's biological advice was published (Bernard 1982). Fifty-five license holders were established; due to administrative delays in regulation changes, a coast-wide quota of 2930 t was set. The full quota was essentially taken from the south coast.

1983: 1981 field sample and commercial catch sample data were published (Breen and Shields 1983 and Harbo et al. 1983, respectively). Managers requested additional resource surveys be carried out as they were concerned that while localized populations were being heavily, and possibly overexploited, the overall stock may be underexploited. Area quotas were reestablished at 1982 levels and descriptions of management units changed.

Assessment of Management

Regulation of the geoduck fishery was initiated at a time when much about the biology of geoducks was unknown. Currently, management is both preventive and research-oriented in rationale. Landings are controlled by a quota at what is still felt to be a conservative level (Harbo et al. 1986), and quotas are being used to encourage fishermen to exploit new areas. In so doing, they provide through log books data on the abundance and spatial characteristics of the resource.

While the professed overall goal of management today may be for OSY, this has not always been the specific management objective identified for the geoduck fishery. In 1979, the following was stated (Shellfish Res. Board 1979, unpubl.):

> "Most of us have been under the impression that our Department's policy was to seek to optimize the use of fisheries for the benefit of their users . . . |the Director-General| pointed out that there is no basis in our mandate for that policy. Our mandate states that it is our job to *conserve*, *preserve* and *protect* the fisheries resource."

The present objective is to stabilize landings at approximately the maximum sustainable yield (R. Harbo, pers. comm.), in contrast to a management proposal in the early years of the fishery that geoducks, because of low and sporadic recruitment, were effectively a non-renewable resource and could be "mined".

This management proposal was not accepted because of some strongly argued views that geoducks could and should be managed on a long-term, sustainable basis. The view today is that existing biological information about this species remains limited (Breen and Shields 1983; Harbo and Peacock 1983), 9 years after the fishery commenced. Scientific studies carried out in British Columbia in recent years have produced results which, while they confirm and to a certain extent refine, previously held views, essentially provide no new biological options for management. Existing quotas were established on virgin biomass values of questionable quality, and while they restrict overall exploitation of the stock to a conservative level, individual concentrations within statistical districts are being exploited extremely heavily (R. Harbo, pers. comm.). Effort control only limits the number of licensed vessels. Accurate resource surveys can only be carried out with divers and because of sampling difficulties and the wide occurrence and patchy distribution of the species, an accurate biomass survey for the coast will be costly to effect (Sloan 1985).

CASE HISTORY #3: ABALONE

Biology and Fishery

Northern abalone (*Haliotis kamtschatkana*) are gastropods widely distributed from California to southeastern Alaska, and from the intertidal to a depth of 15 m in British Columbia. They reach sexual maturity at about 3 yr, or 50 mm in size, and unlike geoduck, cannot be aged from growth rings. However, in a good habitat it is estimated abalone may reach the minimum legal size of 100 mm in 6–8 years. Maximum age is estimated to be about 15 years, or 140 mm in size (Fedorenko and Sprout 1982).

Duration of the larval period (10–12 days) is relatively short in comparison to most other regionally exploited species.

The current commercial fishery began in 1976 and exploitation has been intense, with few abalone now found larger than 110 mm in heavily exploited areas (Boutillier et al. 1984, 1985). Published annual landings differ considerably, depending upon whether sales slip and/or fisheries log information is utilized (e.g. Annual B.C. Catch Statistics, Statistics Div., Field Services Branch, Dept. of Fisheries and Oceans; Farlinger and Bates 1985), but regardless of source, annual landings (Fig. 3) have decreased consistently since 1977 (Fedorenko and Sprout 1982). In recent years, prerecruit abalone abundance in some major fishing areas has decreased significantly (Boutillier et al. 1984, 1985). The 1984 landing was 56 t and consideration is being given to further restricting the fishery for conservation reasons; poaching is a concern. Fishery value was $462,000 in 1984.

Chronology of Biological Advice and Management Decisions

(1975–1980: Fedorenko and Sprout 1982; 1981: Sprout 1983; 1982: Bates 1984; 1983: Bates 1985):

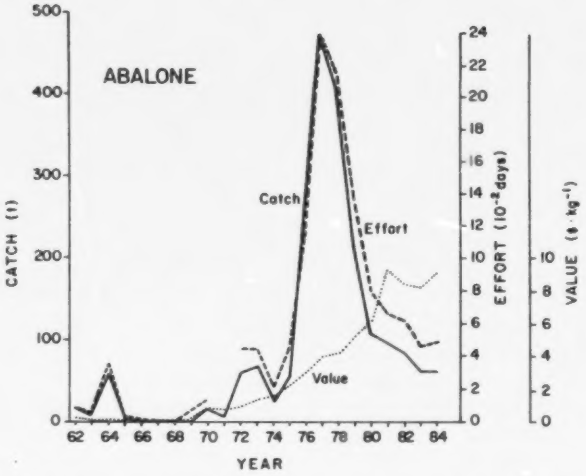

FIG. 3. Annual catch, effort and unit price for the British Columbia abalone fishery. Source: 1962–1976: Annual B.C. catch statistics, Statistics Division, Field Services Branch; 1977–1984: Farlinger and Bates 1985.

1975: No effort or catch restriction existed; minimum legal size was 64 mm width (= 90 mm length) and although the fishery was still relatively undeveloped, some 20 vessels participated.

1976: The fishing season was shortened to 10.5 months after a catch increase of 480% in one year: 43 participants.

1977: Minimum size limit was set at 100 mm length to afford better protection of abalone stocks, based on earlier growth and reproductive data (Quayle 1971). Limited entry was established, with 29 licensed participants and a maximum of three divers per vessel. Some area closures were established for social reasons and season length was reduced to eight months.

1978: Season length was shortened to 3 months since earlier controls did not limit catch.

1979: Catch was still relatively high and on the basis of an estimate of maximum sustainable yield for the whole coast of 115–150 t (Breen 1980), and on an assumption that not all populations had yet been fished and that the biomass estimate (Breen 1980) was conservative, a quota of 227 t was imposed. A total season length of 7.5 months was permitted. It was pointed out that an accurate survey of coast-wide abalone biomass could not be carried out because resources were too limited. Studies were initiated to assess whether apparent low abundance of prerecruits was a real biological phenomena or a result of poor survey sampling design.

1980: Further restriction was imposed by reducing the quota 50% to 113 t on the basis of a suggested real decline in prerecruit abundance and a revised evaluation of MSY (Breen, unpubl. data); the quota was divided equally among licensed vessels.

1981: On the basis of anecdotal information, further revision of MSY estimates (Breen, unpubl. data) and declining CPUE, the quota was further reduced to 94.4 t. It was now suggested that because populations were so contagiously distributed and stock biomass was so low, effects of fishing on stock size could no longer be statistically assessed on an annual basis because of high sample variance arising from a contagious pattern of distribution.

1982: No new biological advice was presented, but the confidence of earlier MSY estimates was questioned because of the extreme sensitivity of the model to changes in parameter value estimation. The quota remained at 94.4 t.

1983: Increasing concern about (1) the validity of assuming constant recruitment and mortality in earlier analyses, (2) anecdotal information about higher than anticipated prerecruit fishing mortality, and (3) concern now being expressed by fishermen of stock declines, resulted in a quota reduction to 70.8 t. A survey of prerecruit and recruit abundance in a major fishing area was initiated.

1984: Continued CPUE decline, a decline of about 50% in both prerecruit and recruit abundance from 1979-80 levels (Boutillier et al. 1984) and concern by fishermen resulted in a quota of 59 t (2.3 t per fisherman). This was to be reduced to 47.2 t (1.8 t per fisherman) in 1985.

Assessment of Management

No detailed documentation of the objectives of management is available for the early years of the fishery. The 1978 regional mandate described in the geoduck fishery analysis would have applied to abalone, although this policy was apparently not followed by managers (Sprout, pers. comm.). It was stated (Shellfish Res. Board. 1979, unpubl.):

"We aim to stabilize catch at 113.4 t yr^{-1}".

and while quota reductions were planned, they were to be step-wise in small increments to minimize the negative economic impact on fishermen. However, hindsight has shown that with earlier heavy exploitation, and poor recruitment in recent years, this was not an effective strategy at that time in stabilizing landings. Managers were reacting to declining abalone abundance by decreasing catch quotas, and in the early years, decreasing effort (number of licensed vessels). However, because of a general lack of knowledge about abalone biology and pressure by fishermen to maintain landing levels, the required major reduction in fishing needed to stabilize landings was not identified or effected. Today it is recognized that the pre-1979 fishery was harvesting accumulations of older animals, and that recruitment is generally low; earlier high annual landings were far above the sustainable annual abalone yield (Fedorenko and Sprout 1982). Present evidence of continued low recruitment (Boutillier et al. 1984, 1985) suggests that recruitment over-fishing may have occurred, and this is now recognized as a real hazard in intensive commercial abalone fisheries. Relatively limited dispersal of larvae may be a compounding factor, as it may limit the ability of remote populations to rebuild locally depleted ones. Overfishing was apparently one of the major causes for a severe decline in abalone abundance in California, despite appropriate and enforced size limits (Cicin-Sain et al. 1977), but even with this example, Canada has not been able to establish a stable fishery at this time. Managers did not initiate required actions in time and researchers did not provide relevant advice which clearly outlined the consequences and risks associated with alternate management options.

The British Columbia abalone fishery is a poignant example of a situation which can arise when a significant fishery is established at a time when little prior information is available on stock status and species population dynamics. How detrimental this will be to future recruitment is presently unknown. While there is some evidence in other abalone fisheries that recruitment overfishing can occur, low levels of recruitment in British Columbia in the early 1980's occurred with a high parent population at the time of spawning, and a reduced legal-size population (because of high landings in the early years of the fishery) during their juvenile and early adult stages. Such conditions alone would seem to favour high survival and subsequent recruitment, but since this has not occurred, other factors, presumably environmental, seem to have been of primary importance. Whether or not abalone abundance in British Columbia cycles over the long-term is unknown, and it may have been that the fishery just happened to commence before a natural decline in abalone abundance was to occur. Continued monitoring of abalone abundance over the long term is required before recent population fluctuations can be interpreted with confidence.

CASE HISTORY #4: PRAWN

Biology and Fishery

Prawn (*Pandalus platyceros*) are British Columbia's largest shrimp, and in part because of their common occurrence in many sheltered inlets, landings of this species have increased from 70 t in 1976 to 380 t in 1984. Becaue of their benthic habit and preference for rocky slopes, prawn are traditionally fished with traps at depths of 20-200 m. Prawn are protandric hermaphrodites and are males at 1-2 yr of age and females at 3-4 yr of age. While this aspect of their life cycle is reasonably well understood (Butler 1980), stock definition and early life history have not been studied in detail. Fisheries research studies have only been initiated during the last few years and much remains to be addressed.

The fishery (Fig. 4) has grown dramatically in the last few years, partly as a result of expansion into inlets in northern British Columbia and in part because of increased effort resulting from the recent decline in salmon landings. At present, no limited entry exists with prawn and many predominantly finfish fishermen now fish prawn in their off-season because of its high landed value. Recent decreases in reported landings are felt

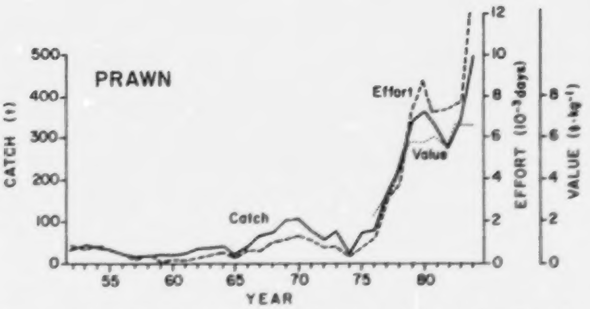

FIG. 4. Annual catch, effort and unit price for the British Columbia prawn fishery. Source: 1953–1983: Annual B.C. catch statistics, Statistics Division, Field Services Branch; 1984: D. Noakes, pers. comm.

to be an artifact arising from increased undocumented private sales. Reported landed value in 1984 was $3.3 million.

Chronology of Biological Advice and Management Decisions

pre-1979: No management. Prawn reseach was initiated in 1974 in one inlet to monitor the population dynamics of a known exploited stock (T. Butler and J. Boutillier, unpubl.). Exploratory studies of general prawn distribution north of Cape Caution and in offshore waters were initiated.

1979–82: Criteria for evaluating stock status were established based on relative female abundance indices and stock status was monitored in about one-third of exploited inlets. Research effort decreased because of time commitments to real-time monitoring of stock status.

1983–84: It was recognized that stock monitoring required more resources than was regionally committed. As a result, many areas were not well monitored and overfishing in some inlets may have occurred. Research has focussed on standardizing gear performance to allow better evaluation of commercial log book data.

Assessment of Management

In its recent history, management of this fishery has followed a common pattern. Initially implemented by researchers, management became so time-consuming as the fishery expanded that it was disrupting their ability to undertake research. As a result, management responsibility was transferred to designated resource managers, who, because they were already fully occupied in managing other fisheries, also had difficulty in providing an acceptable level of management, which was worsened by significant fishery expansion. There are currently in excess of 300 active fishermen, and while official statistics may suggest that landings have recently declined, resource managers estimate that a significant proportion of landings are unreported and landings are increasing. The real challenge will be to learn from the experience of the abalone fishery and quickly establish realistic management objectives which can be readily achieved and evaluated. This will have to be initiated with limited biological advice.

To date, no clear management objectives have been established and each inlet's population is being exploited as if it were a separate stock. With many landings unreported, the best measures of stock status are proportion by size (i.e. age, or sex) and CPUE, but to establish either index requires a significant resource commitment. Currently, the main management issue is the landing of "small" prawns, and there is concern that because female prawn, being larger than males, are heavily exploited, the potential for recruitment overfishing for this crustacean is high.

The British Columbian experience

A number of general observations can be derived from the above four case histories, which while perhaps most relevant to the British Columbian situation, I suggest are common to many worldwide fisheries management situations:

1) *Rate of change*: A resource can change rapidly from an apparently stable state to a depleted one, as has been discussed by Gulland (1971) and Garrod (1975), and this change is difficult to detect until it has been completed and is quite obvious. This has been suggested to result in part from both technical uncertainty and a lack of clearly-defined biological criteria for establishing resource state (Garrod 1975). With most, if not all, fisheries, stock:recruitment relationships are uncertain and in many, exploitation is so intense that few individuals survive more than a year or so after recruitment to the fishery. Short-term stock status is thus best predicted by prerecruit abundance. However, for many declining invertebrate fisheries, timely information is frequently difficult to obtain with sufficient precision to justify early preventive management action. The juvenile stages of many species are often secretive or cryptic, are found in different habitats from adults, and are often not effectively sampled by commercial fishing techniques. Many species recruit only a few years after hatching and because of patchy, extensive distributions, it is often operationally difficult to establish recruited biomass, let alone relative abundance of juvenile cohorts. In addition, commercial CPUE often remains relatively high until a stock is seriously depleted, since it is more a reflection of the availability, or number, of concentrations of adults rather than average density within a population. Irrespective of whether a decrease in stock abundance is the result of environmental factors or overfishing, its manifestation under intense exploitation can lead to major invertebrate fishery decline within only a a few years.

2) *Management development time-frames:* Management of invertebrate resources has in many cases only been initiated within the past decade. An approach to achieve initial conservative management in the development of a new fishery has been described (e.g. Hancock 1979), but the time duration over which such conservative practices should be applied must be con-

sidered in the context of two factors: average age at which individuals recruit to the fishery and the way in which management was initiated. If prerecruit abundance is difficult to assess and the possibility exists that recent recruitment to the population may be lower than assumed, the duration in time over which initial conservative management should extend should well exceed the average age of recruitment to the fishery of the species being managed. It is not always possible to ascertain whether a newly exploited fishery is above or below historic average abundance, and in what direction a natural fluctuation in biomass is likely to proceed in. Initial conservative management did not occur with abalone in Canada, and since individuals recruit at an estimated age of 6–8 years, the first real indication of stock depletion after extensive exploitation might take 6 years to manifest itself. Unfortunately, while quotas were by then at a level initially estimated as sustainable for the original perceived population size, actual biomass was then much less, and in the absence of any effective stock assessment technique, high exploitation may be continuing.

If establishment of a new fishery is proposed by researchers and managers, perhaps as a result of resource surveys, then control of fishery development theoretically can be exercised from the onset. If, however, as was the case again with abalone and is the situation with prawn at the present, a developing fishery experiences a period of uncontrolled expansion before restrictive management is introduced, then real attention should immediately be addressed to the likelihood that future stock status may already have been negatively affected. By taking advantage of the clarity of hindsight, it is possible to state now that abalone management action in the late 1970s should have considered this possibility and been more restrictive until a level of exploitation representing maximal exploitation was better defined.

3) *System-imposed response limitations*: Management philosophy was introduced relatively suddenly for most British Columbian invertebrate fisheries in the late 1970s, and with the problems besetting salmon fisheries at that time, no new resources were directed to invertebrates. Most regional invertebrate fisheries were relatively small and were considered not too important at the time. The result was twofold: (1) scientists were suddenly being asked to provide management advice on species about which little was known biologically, and the number of species being considered for management became so great that only limited study could be devoted to any one species; (2) prior research experiences of biologists studying invertebrates in the 1970s was largely ecological and behaviour oriented and involved relatively little use of analytical methodology. Requirements of contemporary management procedures demanded new skills, including familiarity with computers, which took time to be learnt and applied. The absence of any forum for discussion of stock assessment practices further delayed the extent and sophistication with which new approaches were introduced. Initial management should thus again have been particularly conservative so as to allow for experience to be acquired.

Another element was that because management objectives were poorly defined, both in the minds of managers and researchers, the nature of options available to them and their resulting implications may not have been fully realized. Attempting to control effort can involve so many regulations as to be cost-ineffective (e.g. Gulland 1983) and often managers have only certain ways open to them by law by which fishing activity can be restricted. In some jurisdictions, limited entry is prohibited, but even in places such as Canada where it is technically possible, the process of introducing or modifying a regulation can often take a number of years to effect. In the meantime, significant resource depletion can occur. Additional risks generated by such system-imposed limitations have to be recognized and accounted for.

4) *Implications of Management on Research*: Management by its demands on researchers influences the type of activity which scientists carry out. Demands for stock assessments and descriptions of the state of the resource result in increased effort devoted to stock monitoring versus more investigative research. This was recognized by Garrod (1979), who described it as a "chicken and egg" situation where researchers are aware of the technical deficiencies of their science but are unable to deploy sufficient research effort to upgrade it and thereby perhaps minimize monitoring demands. This was the situation with prawns in British Columbia in the early 1980s.

In addition to requiring time, management of a resource can greatly influence both the type and quality of data made available for scientific analysis. This was documented for the Western Australian rock lobster fishery (Morgan 1980a, b), where because comprehensive catch statistics were not collected until serious management began in 1963, the potential for fishing effort to actually increase while appearing to be stable could not have earlier been determined. Subsequent analysis has demonstrated that initial regulations, including limited entry, did not fully stabilize fishing effort, which in one phase of the fishery increased 139% over the following 11 years. Recent closures have apparently restricted the potential for further increases in fishing effort, but it was the fortuitous introduction of limited entry in 1963 at a relatively low effort level that prevented later serious overfishing.

In most traditional British Columbian invertebrate fisheries, because management has been lacking or has been effected by minimum size limit only, the collection of accurate catch and effort data has had a relatively low priority. Because of widely distributed, often small landings, accurate data from invertebrate fisheries is often particularly difficult to obtain. Representative subsampling is being planned for a few select species, but there is insufficient past data to clearly evaluate the possible fisheries impacts that fishing practices versus environmental factors may have had.

5) *Future management options*: To date, invertebrate fisheries management in British Columbia has had no clearly defined criteria whereby performance could be readily assessed. The general absence of any clear evidence that fisheries, with current regulations, are major factors determining future recruitment levels, raises the

question as to "How can management do better?". If overall population abundance cannot apparently be controlled, then achieving the most from whatever recruitment occurs is perhaps all that should be desired. For many fisheries, assessment of management should then focus on this perspective rather than trying to achieve a long-term stability in annual landings by controlling exploitation rate.

In British Columbia, invertebrates as a group will likely increase in relative regional importance as market potential of currently under- or unexploited species are realized. Traditionally exploited species, whether finfish or invertebrate, are generally fully exploited, and so while new resources may be available for invertebrate study and management, resource level per species is unlikely to increase. Most invertebrate fisheries, then, will never warrant or command large investments in data collection, monitoring or research, and may never be supported by data bases and assessments adequate for active management. In this sense the west coast fishery is significantly different from that in Atlantic Canada, where sea scallops (*Placopecten magellanicus*), American lobster (*Homarus americanus*) and snow crab (*Chionoecetes opilio*) are all major regional fisheries, and invertebrates in recent years have rivalled both marine and anadromous finfish combined in landed value.

Attempts at establishing a comprehensive, scientifically based management system for each of the numerous small invertebrate fisheries thus becomes a charade, and researchers and managers should be skeptical about believing that they in any meaningful way either understand or can influence to any significant extent future stock abundadnce with acceptable fishing strategies. Research support on any given fishery will be limited and decades may be required before a modest understanding of population dynamics is attained. Restrictive regulations such as quotas or fishery closures may be necessary at somewhat arbitrary levels or dates to control effort or landings until species population dynamics are better understood. It is impractical to develop a common management approach for all invertebrate fisheries because of the diversity in both species biology and fishery type. In those fisheries where most, if not all, animals are lethally damaged during capture, e.g. many shrimp and euphausiid trawl fisheries, geoducks, and squid net fisheries, management emphasis should be on trying to harvest a predetermined percentage of the available biomass. However, in size-selective fisheries where individuals can be released with minimal physical damage, management should focus on optimizing yield and/or egg production from the level of recruitment which occurs, rather than trying to control future recruitment and achieve stability in landings. Management of these latter species will have to largely depend on common sense and elementary, easily enforceable regulations such as minimum size limits. Effort control may be difficult to achieve, and this may tend to cause annual landings to fluctuate more if fewer year classes end up supporting a fishery. However, since most regional invertebrate fisheries are generally recognized as minor, variable effort in these fisheries may not necessarily be bad for the Canadian west coast fishery as a whole. In the absence of limited entry and effort restriction in many minor fisheries, these fisheries may provide needed short-term economic benefits for multispecies fishermen when the region's major fisheries are performing poorly. How to achieve an optimum return in such a multispecies exploitation scenario may ultimately be the real management challenge.

In conclusion, it seems that while many of these observations have been referred to in the literature in one form or another, the reality is that managers and researchers still seem to learn most effectively only from direct experience. Problems documented in other jurisdictions seldom seem to be avoided. Only perhaps by additional documentation and assessment of fisheries management performance can the degree to which this might happen in the future be minimized.

Discussion

While it appears easy in hindsight to identify system flaws and to suggest alternate, perhaps more effective management actions (e.g. Rothschild 1983), it must be recognized that the best efforts of managers and researchers were being made at the time to manage fisheries on the basis of perceived objectives, available advice, experience and system-imposed restrictions and delays. The real measure of the system's performance now depends on how much can be learned from past events and to what extent and at what rate the system can be modified to avoid identified problem areas. Since fisheries and fish stocks are both dynamic systems, it can be expected that new problems will develop even as older ones are being ameliorated, and so this will always be an on-going process.

On the positive side, except for possibly abalone, no invertebrate fishery in British Columbia has been terminated or significantly curtailed as a result of overfishing. There is little, if any evidence that fishing has had any major impact on future recruitment levels, and while annual recruitment has fluctuated over time, environmental factors appear to be the primary causal factors. Minor fishery problems which periodically arise are generally dealt with quickly in an acceptable manner, and the main management concern seems to be that not all resources are being exploited "optimally", although what this exactly means is seldom adequately defined. Biological advice has been used as the basis for most management actions and there is close cooperation between investigative researchers and managers.

Nevertheless, some concerns which can be concluded from our experiences in British Columbia and which often apply regardless of fishery location, are as follows:

1) *Better definition of management objectives*: From discussions with policy planners, resource managers and researchers, it is evident that perceived objectives of management differ and that no clear, specific goals have been or are presently identified on a fishery by fishery basis. A national policy for Canadian fisheries has been discussed (Anon. 1976) and 25 strategies identified as guidelines for program design, but since priorities vary so much by both fishery and region, it is still largely left to locally mandated personnel to iden-

tify and priorize objectives. These are invariably poorly communicated to others, seldom documented, occasionally contradictory and are often ephemeral in duration, making it virtually impossible to determine if goals are either achievable or achieved. It is difficult to measure progress when no direction is provided.

2) *Develop methodology to establish research priorities objectively*: This concern was addressed (Table 3) in a recent workshop on the scientific basis for the management of penaeid shrimp (Rothschild and Gulland 1982), and methodology has been proposed by Healey (1984) and others. It is particularly relevant here in British Columbia where numerous problems for many species need addressing by limited scientific and managerial resources. There is evidence that the system reacts to crises, but little evidence that it anticipates them and minimizes deleterious consequences by utilizing available resources most effectively. While management and research concerns can be expected to vary on a regional basis, methodology to establish priorities acceptable to all parties should have general application.

3) *Formalization of a management review process*: As was alluded to earlier, the perceived priorities of investigative researchers and managers often differ, and in the absence of a defined management infrastructure, biological advice may appear ad hoc and lack focus. Who priorizes and asks for biological advice, and ultimately receives it, is an important element often overlooked. Individuals all have their own biases, and if research and management personnel are in different lines of authority operationally, conflict situations may occur.

One solution is to establish a management committee with balanced representation from relevant groups. This allows each group to present its arguments for specific programs, and provides a clearly defined authority and forum to evaluate progress and recommend further action. This is particularly important in situations such as invertebrate management where a number of alternate options are often available, and because of limited research and management resources, choices between which fisheries are studied at any one time may have to be made.

4) *New methodology for improved assessment of resource status*: As indicated above, it is generally difficult with widely distributed, secretive species to establish stock status and determine degree of resource utilization (under- or over-exploited) in a timely manner. The combination of unique biologies, variable fishing techniques, and environment-induced fluctuation makes application of general criteria for invertebrates questionable. Development of new methodology such as experimental fisheries management [e.g. the actively adaptive probing strategies of Smith and Walters (1982) and Ludwig and Hillborn (1983)] may be required to better document the interaction between management strategy and species biology, although since the livelihoods of individuals are involved, care has to be exercised in creating manipulative situations. With British Columbian prawn, it is currently planned to develop six, discrete research study areas where exploitation would be only by special permit, would be well-documented and would be designed to achieve a specified stock status to facilitate investigation of the consequences of alternate management actions. The existence of scores of small, apparently distinct populations in inlets along the coast makes this species particularly amenable to such experimental study, but for most species, such experimental management opportunities are generally much more limited.

5) *Facilitate a multi-disciplinary approach to management*: The ad hoc introduction of new regulations designed to counteract flaws or unanticipated effects in previously introduced regulations demonstrates clearly the tendency of managers and researchers to

TABLE 3. An example of decision analysis of research priorities for the USA penaeid shrimp fishery (modified from Rothschild and Gulland 1982).

Research objectives	Management Objectives: Optimum size	Max. economic function	Min. biol. risk	Habitat mgmt.	Total score	Mgmt. need rank	State of knowledge rank**	Ranked total score	Combined rank
Growth	1*	3	2	3	9	6.5	H/9	15.5	9
M	1	3	2	3	9	6.5	L/3	9.5	4
F	1	1	1	2	5	1	M/4	5	1
S/R	2	2	1	2	7	3.5	L/2	5.5	2
Interspecies relationships	3	3	1	1	8	5	L/1	6	3
Environmental interactions	2	1	2	1	6	2	H/8	10	5
Harvesting economic dynamics	2	1	3	1	7	3.5	H/7	10.5	6
Processing economic dynamics	3	2	3	2	10	8	M/6	14	7.5
Market economic dynamics	3	2	3	3	11	9	M/5	14	7.5

**Score description* — 1 = essential; 2 = primary supporting information; 3 = secondary supporting information.
***Level of current knowledge* — H = highest; M = moderate; L = least.

view resource development decisions as short-term choices among a series of alternatives. Consequences of failing to recognize that decisions today may influence options in the future has been discussed by Walters (1975), and future option foreclosures should be considered. This field of research is outside the theory with which most biologists are familiar and it demonstrates the need to involve experts from a number of disciplines in the management process.

Similarly, treatment of measurement error and uncertainty in parameter estimates poses real difficulty in interpreting data, yet with few exceptions (e.g. Ludwig and Walters 1981), consideration of such problems has not been addressed, not because they were unrecognized but because insufficient mathematical expertise has been available. Significant advances in other disciplines have occurred and with use of modern computers, research and analyses can be conducted today which would have been impossible even a decade ago. Involvement of such expertise from other fields must become a more integral part of future research activities if fisheries science is to make real gains.

6) *Establishment of an international forum for discussion of Pacific invertebrate research initiatives*: It is no coincidence that the highest research priority is generally directed to species where a high political priority has been assigned to maintaining fisheries stability. Research on finfish has predominated, reflecting the relative value of different fisheries, the degree of capital investment and the success with which different interest groups have argued their concerns. Pacific invertebrates, excluding king crab, have received relatively little attention historically.

However, with most traditional, regional fisheries now largely fully exploited and high prices paid for many quality invertebrate products, better utilization of existing resources, and perhaps even their enhancement, is now being advanced. Many fishermen now fish both finfish and invertebrates, and there has been increased interest in invertebrate aquaculture for a number of species throughout the Pacific. To minimize duplication of research, establish improved dialogue, and facilitate documentation of progress, a formalized forum for discussion of Pacific invertebrate fisheries research, stock assessment, management and aquaculture issues is advocated. I suggest that its establishment will significantly and positively enhance the harvest from invertebrate fisheries and like ICES (Gulland 1982), permit regional coordination in addressing unique Pacific fisheries interests.

Conclusion

If the claimed objectives of fisheries management in British Columbia, to manage, conserve and enhance fished stocks for the greatest possible benefit from renewable fishery resources, are to be realized, procedures to evaluate and learn from the consequences of past and present management actions must be facilitated. The complexity of issues and frequent turnover of staff characteristic of any large bureaucracy demand that timely review and documentation of management advice and actions be implemented. In British Columbia, a formalized process to achieve this is *required*.

Finally, the diverse biologies and fishery characteristics of commercial invertebrate species impose unique stock assessment and management situations. Strategies suitable for one fishery are often not appropriate for another because of variable data type and quality. Stock recruitment relationships are uncertain and precise estimation of stock biomass is often impractical. Active management of invertebrates should only be initiated if resources to effect them are available. This is not the present situation with some invertebrate populations in British Columbia. Conservative catch or effort quotas to restrict a fishery while either the basic population dynamics of the species are being determined or the status of the resource is being assessed may be required, and an expectation of maximal resource utilization during this period is unrealistic. Years, perhaps decades, must be allowed to document long-term population responses to both biotic and abiotic perturbations if ongoing, optimal exploitation is to be achieved.

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SAMPLING OF ADULTS, JUVENILES, AND LARVAE

Commercial Fishery Data Isopleths and Their Use in Offshore Sea Scallop (*Placopecten magellanicus*) Stock Evaluations

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Exploitation of a major sea scallop (*Placopecten magellanicus*) resource has occurred for decades on Georges Bank in the Western Atlantic. The latest series of Canadian stock evaluations began in 1977 with randomly stratified sampling and strata assigned according to fishery catch. Survey design now utilizes strata described by isopleths of commercial CPUE. Because sea scallops are contagiously distributed, Canadian offshore scallop surveys are directed toward concentrations of this species.

Pertinent commercial fishery information, including landings, effort variables, and location on the Bank, are recorded accurately in fishing logs. Isopleths of fishery parameters can be established by joining points of similar value to describe the spatial pattern of exploitation in relation to the resource.

The high CPUE stratum is relatively heterogeneous, including areas of particularly high scallop density. Up to 70% of the survey area had a very low to zero exploitation level.

Resource surveys provide standardized survey catch-rates (number of scallops at-age per tow). Isopleth mapping is used to establish overall abundance at age and to describe spatial patterns of scallop aggregations.

The coefficient of determination between annual Canadian commercial catch and the recruited biomass estimated from research vessel surveys is 0.89 for the 1978 to 1983 period. Survey results have been used to monitor stock status and the value of the present survey design is discussed from both a management and research perspective.

Depuis des décennies, a lieu l'exploitation commerciale d'une importante source de pétoncles ou pectes géantes (*Plactopecten magellanicus*), sur le banc Georges dans la partie ouest de l'Atlantique. La plus récente série d'évaluations des stocks canadiens a commencé en 1977; à cette époque, ont été organisés des échantillonnages à stratification aléatoire, et les strates ont été assignées en fonction des prises de pêche. Dans les relevés actuels, on utilise les strates décrites par les isoplèthes des prises commerciales par effort unitaire (CPUE). Les relevés des populations de pétoncles au large des côtes canadiennes sont axés sur les concentrations de pétoncles, puisque leur distribution est contagieuse.

Dans les relevés des pêches, est consignée avec précision l'information appropriée sur la pêche commerciale, en particulier les prises, les variables relatives à l'effort, et l'emplacement des mollusques sur le banc Georges. On peut établir des isoplèthes des paramètres relatifs aux pêches, en joignant les uns aux autres les points d'égale valeur, de façon à décrire la distribution tridimensionnelle de l'exploitation en fonction de la ressource étudiée.

La strate élevée de la CPUE (prises par effort unitaire) est relativement hétérogène, y compris les zones de densité particulièrement élevée de populations de pétoncles. Dans une proportion atteignant 70% la zone de relevé était caractérisée par un taux d'exploitation très faible à nul.

Les relevés des ressources nous donnent les taux de prise normalisés (nombre de pétoncles à maturité par dragage). On emploie les cartes d'isoplèthes pour établir l'abondance globale à maturité et pour décrire la répartition tridimensionnelle des agrégations de pétoncles.

Le coefficient de détermination entre les prises commerciales annuelles du Canada et la biomasse recrutée, estimée d'après des relevés obtenus par les navires de recherche, se situe à 0,89 pour la période 1978–1983. On a employé les résultats des relevés pour établir le statut actuel des stocks, et l'on étudie la valeur du modèle actuel de relevé à la fois des points de vue de la gestion et de la recherche.

Introduction

The waters of Georges Bank, located in the Northwest Atlantic between Massachusetts and Nova Scotia (Fig. 1), are some of the most productive in the world (Riley 1941; Cohen et al. 1982; Sissenwine et al. 1984) and have sustained a major sea scallop (*Placopecten magellanicus*) fishery for decades. While much is known about sea scallop biology (Serchuk et al. 1979), the wide distribution of commercially exploited concentrations over the Bank (approximately 31 000 km² within the 90 m isobath), their exploitation by two countries (Canada and the United States) in mutually exclusive areas, and the use of different biological survey and

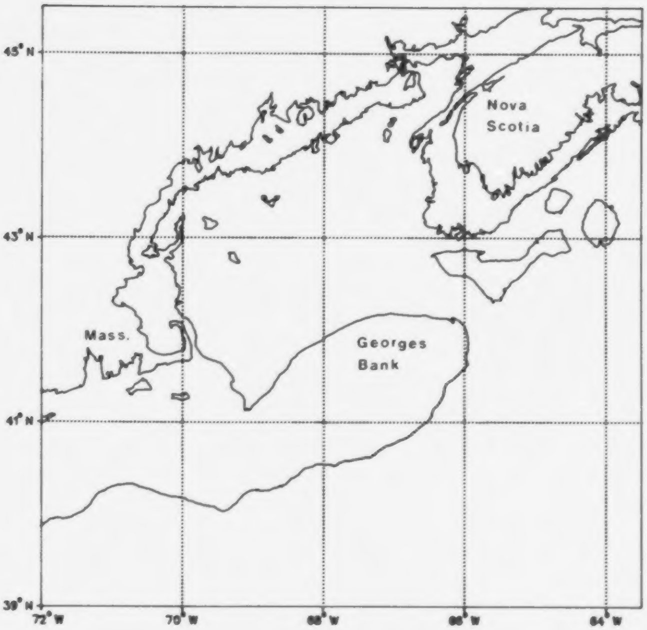

FIG. 1. Georges Bank in the Northwest Atlantic, located between Nova Scotia and Massachusetts. It is delimited by the 100 m isobath on this map.

commercial catch sampling approaches by each country have combined to make estimation of population size and the delineation of the distribution of exploitable concentrations difficult. Prior to 1976, research surveys of scallops on Georges Bank were infrequent and often addressed a specific research goal (e.g., Caddy and Chandler 1966; Caddy and Sreedharan 1971; Serchuk et al. 1979). Resource surveys have been conducted by both countries since 1977, but although the broad objective has been to monitor resource status, such information has not been fully used by both countries in active resource management because of political, economic, and social concerns (e.g., Pierce 1983). Rather, the suggested real value of resource surveys in recent years has been to establish a data base and sampling methodology which better deals with the contagious distribution of commercial densities of scallops. This will allow for more precise documentation over the long-term of the impact of fishing on scallop abundance and distribution, the nature and pattern of scallop recruitment and estimation of growth and mortality rates.

This paper describes the present methodology of establishing Canadian survey strata according to isopleths of fishery data and discusses the research value of this approach in conducting stock assessments and in improving our understanding of scallop biology.

Methods

FISHERY DATA QUALITY

Since the early 1960's, the captain of each vessel has been required to report his daily catch, effort, and location fished. Record keeping is good; logs are complete for virtually every day fished. Logbook entries include vessel name, date, crew size, Loran or Decca readings of fishing locations, water depth, bottom type, number of bags of scallop meats caught per 6-h watch, number of tows made per day, average tow duration in minutes, gear width, and comments. Total catch weight is reported by sales slip. From this data, effort can be calculated according to: (1) days fished; (2) width of gear; (3) tow time (the number of tows per day times the mean tow duration in hours); and (4) crew size (since the catch is manually processed at sea, crew size is important as processing can reduce available fishing time). CPUE ($kg \cdot crhm^{-1}$) is derived from only those data for which catch, fishing location, and effort data for number of crew (cr), tow time (h), and width of gear (m) are available. Daily fishing positions are given by a minimum of two sets of navigational readings with the mid-point of the bearings assumed to be the daily fishing location. Fishermen often keep one bearing constant and vary the other, fishing either along a line or through a common point. Bearings can be determined to an accuracy of 1 s (about 30 m). Since tows average about 25 min duration at 3 knots ($5.5 \ km \cdot h^{-1}$) average tow distance is about 2.3 km (range 1.8–2.8 km). This distance is slightly greater than the axial distance of a one-minute square (OMS) at latitude 42 degrees north (1.38 × 1.85 km). Daily fishing activity was spread (Fig. 2) over the four nearest one-minute squares. Other spreading strategies were evaluated but proved less realistic (Jamieson and Chandler 1981).

More than 95% of the Canadian catch from Georges Bank is accounted for in logbook data. Accuracy is high

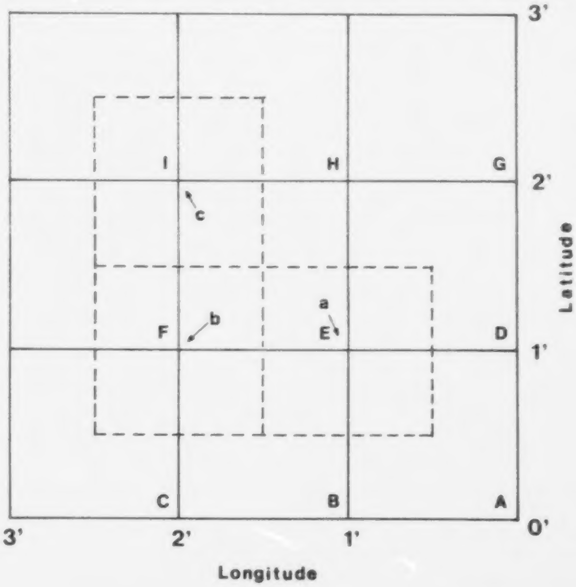

FIG. 2. Illustrations of the method used to assign daily catch from the mid-point fishing location to the nearest position of minute intercept and to spread the data over one-minute (lat.–long.) adjacent areas. For example, the catch of (a), position (1', 1'), would be averaged equally over unit areas A, B, D, and E; of (b), position (1', 2'), over areas B, C, E, and F; of (c), position (2', 2'), over areas E, F, H, and I.

TABLE 1. Stepwise regression of catch versus three measures of catch-rate as independent variables (F^* signif. at 0.0001 level). C.V.: coefficient of variability. Number of cases = 17.

	r^2	C.V. (%)	F ratio*	Partial regression coefficients		
				Non-standard	±95% conf.	Standardized
$kg \cdot cr^{-1}$	0.95742	9.6	337.28	0.010	±0.021	0.503
$kg \cdot h^{-1}$	0.96240	9.4	179.18	21.176	±41.013	0.196
$kg \cdot m^{-1}$	0.96322	9.6	113.49	0.003	±0.010	−0.291

y-intercept: −288.086

(Jamieson et al. 1981), as log records are not used for enforcement purposes.

Canadian catch and expended effort values can be determined for any time period between 1957 and 1983 for any exploited area. A combination of effort variables, including number of crew, towing time, and width of gear, are suggested to best describe the relative performance of the offshore scallop fishery. Standardized partial regression coefficients in a stepwise regression of catch versus CPUE indicated that the crew variable was more than twice as important as the other two variables (Table 1). CPUE expressed as $kg \cdot crhm^{-1}$ was selected as the fishery parameter for isopleth mapping.

Scallop concentrations are of temporary duration, as fishing both reduces scallop abundance and causes scallops to scatter. The seasonal distribution of commercial landings was evaluated to select an appropriate time interval of commercial landings to be used in the determination of strata for a traditionally August resource survey. The historical spatial distribution of fishing locations does not render a realistic mapping of any instantaneous scallop distribution and so only those landings occurring immediately prior to the survey are used in isopleth mapping. The specific time period selected is therefore a function of both recent expended effort and calendar duration. Consequences of varying the number of preceding months used to describe scallop distribution for resource survey purposes was investigated initially by Jamieson and Chandler (1981). Log data from September of the previous year to May of the current year (9 months) is now used. Figure 3 illustrates fishing locations exploited by the fleet from September 1982 to May 1983.

The present boundary of the Canadian survey area (solid black line in Fig. 3) was determined from the historical location of fishing activity. Ninety percent of all locations fished are included within the survey area. Some fishing locations in the southern part of the Bank are excluded; Canadian fishing activity there has historically been slight.

The process of isopleth mapping links points of similar value to generate contour curves of commercial CPUE.

A general purpose contouring program, GPCPII (Calif.

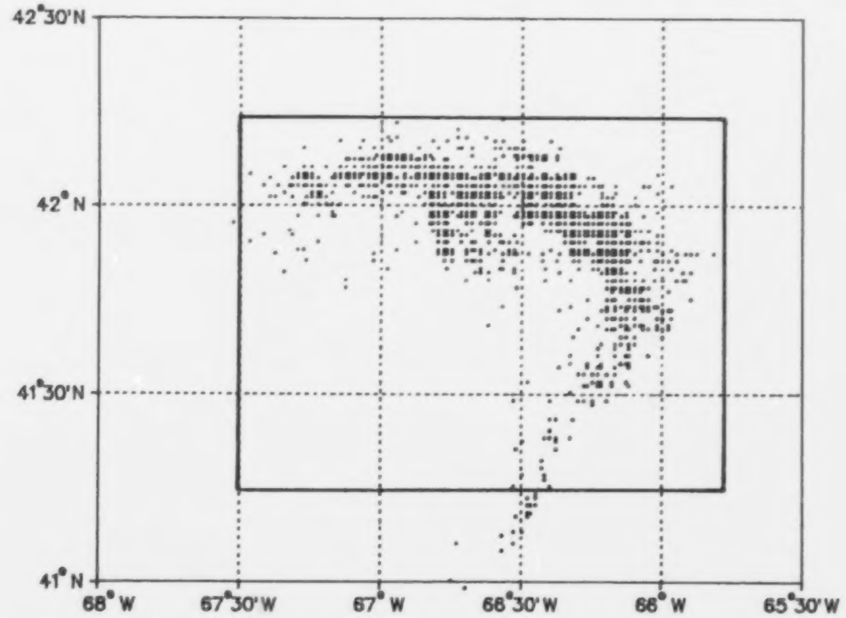

FIG. 3. Fishing locations (one-minute resolution level) exploited by the Canadian fleet for the period Sept. 1, 1982–May 31, 1983 and the area (solid line) investigated during research vessel surveys.

Computer Products Inc., 1972) was used to produce graphic displays. CPUE contours were plotted as closed curves within the boundaries of the overall survey area. The area of each contour was determined using the principles of a polar planimeter. Arbitrary CPUE levels were used to establish strata of high, medium, low, and very low CPUE. Finally, a regular array of data points 2.2 km apart (0.2 degrees latitude) was established from which random sampling locations were chosen for each stratum.

RESEARCH SURVEY

Surveys are carried out with a 2.4 m New Bedford scallop dredge with 75-mm rings and a 38-mm mesh liner and since 1979, are standardized (Jamieson 1982) to a tow length of 800 m (1 951 m^2 per tow). Shell height frequencies for all live scallops caught are measured in 5-mm intervals, and scallop age is inferred from shell height by von Bertalanffy growth curve (Robert et al. 1982).

Isopleth mapping of standardized survey catch-rates is used to establish overall abundance at age for the survey area, using a similar approach to that described above for determining the geographical area of each CPUE stratum. Number of scallops at age per standard tow are converted to density of scallops per square kilometre, which is then multiplied by the area of the stratum.

Results

APPLICATION

Development of a survey design is illustrated for a resource survey conducted on Georges Bank in 1983. Relative indices of abundance-at-age generated by research vessel surveys are also discussed.

The deep-sea scallop fleet (L.O.A. greater than 19.8 m) carried out 1 029 fishing trips in 1982 according to log information. Logs received by the end of May in 1983 documented 329 trips. Daily records from September 1982 to May 1983 with fishing locations within the overall survey area on Georges Bank totaled 5 205 records, with fishing occurring in 1 674 separate OMS areas. The overall survey area includes 5,508 OMS, which indicates that only 30% of the overall area was actually exploited. CPUE values for the 1 674 data locations ranged from 0.013 to 6.358 kg·crhm^{-1}. Fishing was concentrated in the northern section of the survey area and followed the edge of the Bank southwesterly in a broad band. No fishing was reported in the lower left portion of the survey area.

To establish the different strata, distances were converted from decimal degrees to kilometres, estimating the overall survey area as 100.04 by 140.98 km, or 14 104 km^2. CPUE contour intervals were chosen which reflected both the range of CPUE values encountered and an arbitrary, minimum area for the highest CPUE level of 150 km^2 (about 1% of the survey area). Small incremental intervals provide a higher degree of pattern resolution but are more costly in computer time. Computer costs also influence the underlying grid array, which was found to be optimal with a cell size of 3.71 by 2.76 km (10.24 km^2). CPUE exceeded 0.2 kg·crhm^{-1} in only 32% of the survey area; only 12% of the area had CPUE values greater than 1 kg·crhm^{-1} (Table 2). In 1983, landings from the deep-sea scallop fleet on Georges Bank decreased to 2 748 t, the lowest annual landing since 1959 (Mohn et al. 1984). Canadian CPUE for Georges Bank averaged only 0.289 kg·crhm^{-1}.

Caddy and Sreedharan (1971) indicated that traditional fishing practices of the deep-sea fleet were to target their fishing on specific scallop aggregations to obtain a maximum landing. Directed fishing effort causes geographical variations in the distribution of its effects. Since different aggregations often represent specific age cohorts (Jamieson and Chandler 1981) different scallop cohorts may thus experience different fishing mortalities. The assumption of active dispersal to spread local effects of past effort randomly throughout the stock of most fisheries dynamic models does not apply to scallops, and so the empirical estimation of fishing mortality requires that the geographic location of the aggregation, or population, being assessed be identified. The approach advocated in this report takes this into consideration. The mosaic distribution pattern of CEPU (Fig. 4) indicates the contagious distribution of commercial size scallops on Georges Bank and because of the limited mobility of scallops, raises questions as to the usefulness of an average value for any extensive standardized area (e.g., 10-minute square or more of latitude and longitude) of the Bank.

The lowest CPUE strata appears to largely represent areas where no prolonged commercial fishing occurs. Landings reported from these areas were minor and were probably the result of exploratory activity by commercial vessels seeking new scallop aggregations. Survey stations have been allocated to this stratum both

TABLE 2. Estimates of the geographical areas of different commercial CPUE strata on Georges Bank in 1983, and their respective allocations of survey stations.

Min. CPUE level (kg·crhm^{-1})	Area		CPUE strata (kg·crhm^{-1})		Area		% Stations
	km^2	%			km^2	%	
0.0	14 104	100		none		30	—
0.1	9 845	70	0.0–0.19	very low	5 319	38	30
0.2	4 526	32	0.2–0.49	low	816	6	7
0.5	3 710	26	0.5–0.99	medium	1 975	14	23
1.0	1 734	12	>1.00	high	1 734	12	40

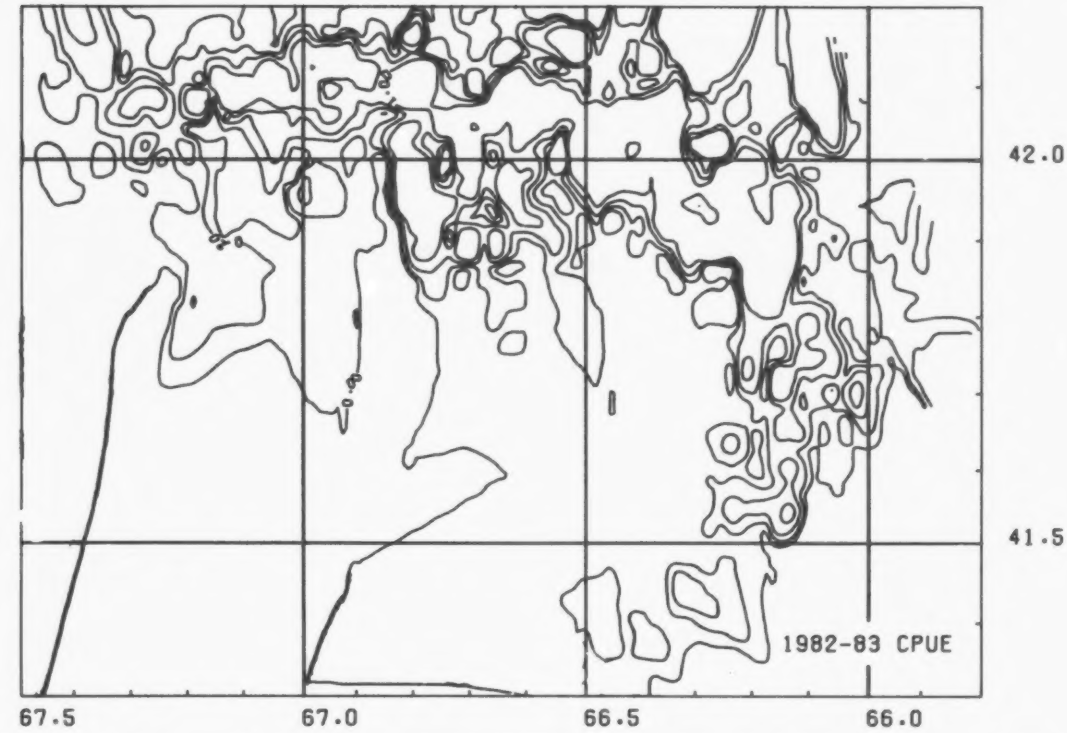
42.0
41.5
1982-83 CPUE
67.5
67.0
66.5
66.0

FIG. 4. Distribution of CPUE-specific areas; commercial catch-rate isopleths are 0.0, 0.2, 0.5, and 1.0 kg·crhm^{-1}. Latitude and longitude are in decimal degrees.

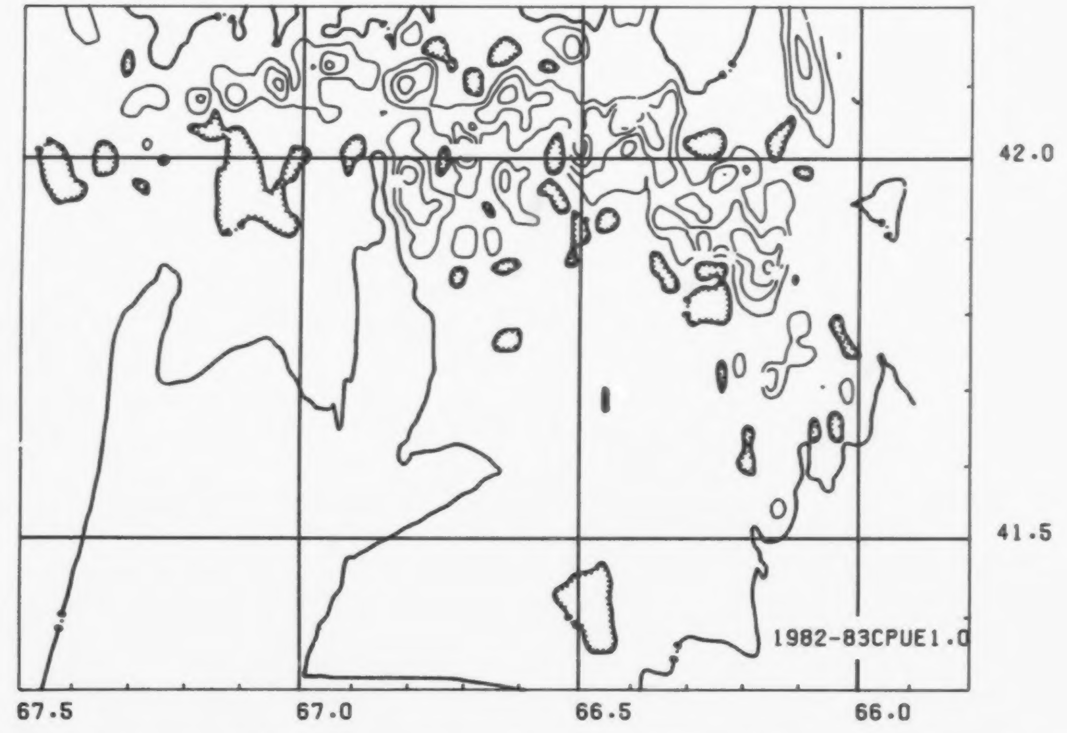
42.0
41.5
1982-83CPUE1.0
67.5
67.0
66.5
66.0

FIG. 5. Distribution of CPUE-specific areas; commercial catch-rate isopleth increments are 1.0 kg·crhm^{-1}, starting at zero. Latitude and longitude are in decimal degrees.

to establish that no major scallop concentrations likely existed and on the off-chance that new aggregations of prerecruit scallops might be detected. However, in the past 6 years that research tows have been allocated to the low CPUE stratum, no significant concentrations of recruits or prerecruits were discovered. This supports our view that unless major resources are available, stock evaluations of contagiously distributed species should not have exploration as their primary goal but rather should concentrate on the characterization of commercially exploited concentrations.

The actual range of CPUE values in the highest CPUE stratum is relatively great (Fig. 5) as it includes areas of particularly high scallop density. Because it is targeted by the commercial fleet, it is of particular interest, and so up to 40% of each year's survey stations have been allocated to this stratum (Table 2). For the other three strata, stations were assigned proportionate to their relative area. The lowest stratum can cover an extensive area, especially in years of low overall stock abundance, and so to allow for a few exploratory tows yet provide reasonable coverage in the other strata, a maximum of 33% of the survey stations are allocated to this stratum.

RESEARCH SURVEY RESULTS

Survey results provide two primary data sets: standardized (research) CPUE values are established at a specific point in time for the major scallop aggregations being commercially exploited, and the size (age) frequencies of these populations are determined.

Isopleth mapping of research survey data is also performed with strate of density at age plotted for the major scallop age classes. The spatial pattern of recent recruitment can thus be depicted (e.g. Fig. 6), and overall abundance at age estimated (Table 3).

Survey abundance-at-age (Table 4) is estimated for a smaller area (10 794 km^2) of the Bank than that used with commercial data. In some years, resource survey

TABLE 3. Estimates of relative abundance of age 4 scallops from the 1983 Georges Bank survey from isopleth mapping of number-at-age per standard tow.

Number per tow	Area (km^2)	Density (10^{-3}km^{-2})	Estimated abundance (10^{-3})
0–10	1 180.036	2.5	2 950.09
10–20	4 231.486	7.5	31 736.15
20–30	283.255	12.5	3 540.69
30–40	468.105	17.5	8 191.84
40–50	504.139	22.5	11 343.12
50–60	225.584	27.5	6 203.56
60–70	187.223	32.5	6 084.74
70–80	127.812	37.5	4 792.95
80–90	87.852	42.5	3 733.73
90–100	47.030	47.5	2 232.90
100–150	132.068	62.5	8 254.25
150–200	61.820	87.5	5 409.25
≥200	34.039	100.0	3 403.90
			97 877.17

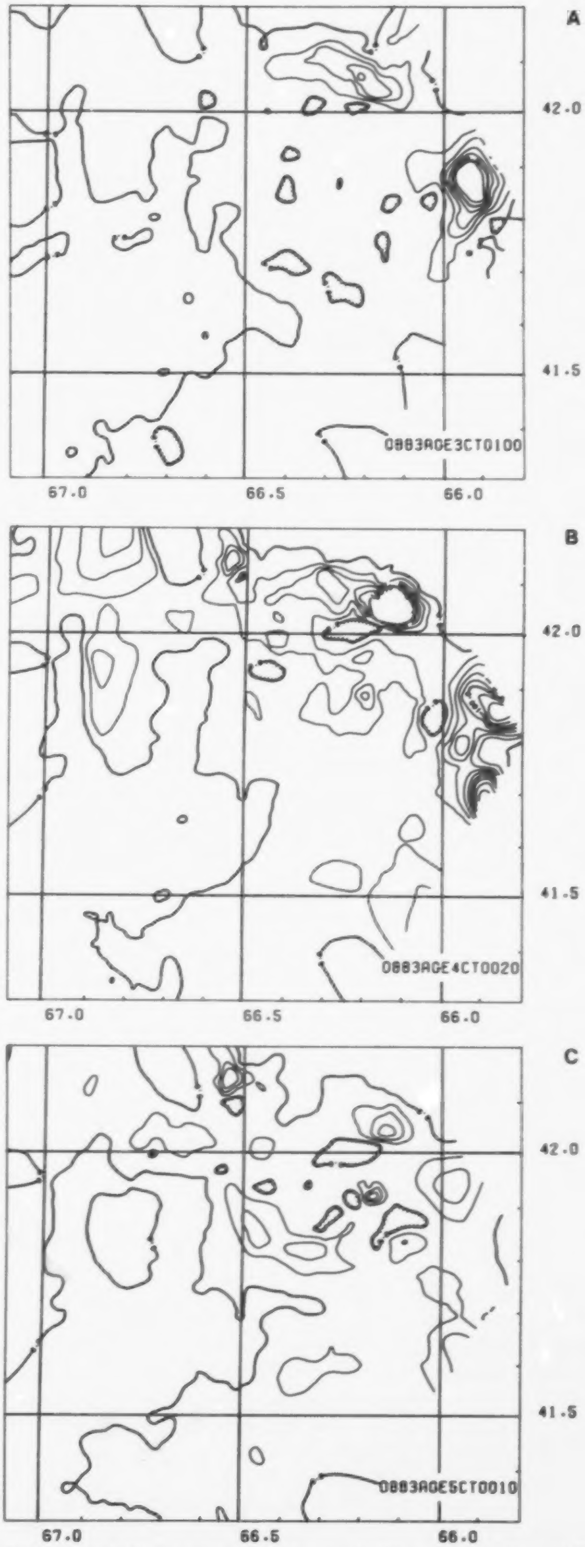

FIG. 6. Isopleth mapping of (A) ages 3, (B) 4, and (C) 5-yr-old scallop distributions in 1983, the isopleth intervals, starting at zero, being 100, 20, and 10 scallops, respectively by age, in a standard tow.

TABLE 4. Estimates of abundance at age (10^{-6}) determined by isopleth mapping of research survey CPUE.

	Age (yr)						
Year	2[a]	3	4	5	6	7	8
1978	781.15	370.39	834.23	326.25	95.21	36.39	11.74
1979	106.18	327.06	184.39	137.46	44.97	22.71	8.25
1980	350.50	181.55	38.58	19.54	14.37	—	—
1981	548.31	551.89	137.31	66.98	—	—	—
1982	241.77	430.42	98.11	23.43	5.09	—	—
1983	204.16	115.75	97.88	24.27	9.52	—	—

[a] Values are underestimated because of reduced gear selectivity.

time was reduced because of bad weather, equipment failure and/or rescue work, and fewer stations were sampled. To make all survey data comparable between years annual abundance estimates are determined for this reduced survey area.

EVALUATION

Comparison with American survey results (Serchuk et al. 1979; F. Serchuk, unpublished data) indicates that surveys from both countries detect major changes in the exploited population: if a scallop year-class strength is exceptional, it is identified, and trends in overall fishery performance correlate well with average research tow CPUE patterns.

The major difficulty in comparing the relative ability of these alternate survey designs to estimate actual scallop abundance is in developing a third, independent assessment technique against which resource survey results can be evaluated. Cohort analysis is one potential approach. Population numbers-at-age data (Mohn et al. 1984) corroborate the depressed stock situation outlined by the abundance indices isopleth-mapping analysis. Table 4 indices of abundance are also decreasing, especially recruited age-classes; the gradual removal of large scallops and no significant improvement in recruitment matches the poor catch levels recorded recently. A coefficient of determination of 0.89 has been found between the Canadian catches from this area (from 1978 onward) and the recruited biomasses estimated from the survey indices of abundance at age.

Increasing the accuracy of estimates of scallop distribution and density is important to fisheries management. Caddy (1975) initiated this process in his spatial model (YAREA) by assuming recruitment in patches of random size and location, and effort expended within each statistical area (one 10-minute square) according to the available biomass alone or in combination with traditional fishing practices. Isopleth mapping shows the contagious nature of scallop recruitment and relates catch-rate patterns at the OMS level to the exploitable biomass. When a longer historical data base is available, one will be able to address such fundamental issues as what is the perceived stock-recruit relationship, how does fishing affect indirect scallop mortality and distribution, and which environmental factors appear to most influence settlement and survival.

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Management and Assessment of Eastern Bering Sea King Crab Stocks

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Research on the biology of red king crab (*Paralithodes camtschatica*) dates from 1940 in North America but has a longer history in Asian waters. Bristol Bay red king crab have been systematically and consistently surveyed since 1969. Research on blue king crab (*P. platypus*) has a shorter history and populations have been routinely surveyed since 1974. Population estimates and biological information from trawl surveys are used in conjunction with fishery statistics as the basis for management of both species. This paper describes methods of integrating survey and fishery data, interpretation of resultant information and how information is used by management.

Survey and fishery data show strong fluctuations in abundance of both species. Peak abundance of commercially exploitable red king crab in Bristol Bay was estimated at 46.6 million crab averaging 2.9 kg in 1979 but had fallen to 1.5 million crab by 1983 when the fishery was closed. Fishery data corroborate survey data and indicate large fluctuations in red king crab abundance during the past 30 yr. Blue king crab stocks show fluctuations of about one order of magnitude and have also declined drastically since 1979. Fluctuating abundance and recent declines have occurred despite management policies intended to promote stability and estimated exploitation rates that never exceeded 60% of legal males or at most 10% of the Bristol Bay population. Declines in abundance are attributed to a combination of high natural mortality and variable year-class strength rather than inadequate management measures.

Des recherches sur la biologie du crabe royal (*Paralithodes camtschatica*) sont effectuées depuis 1940 en Amérique du Nord et depuis plus longtemps encore en Asie. Le crabe royal de la baie Bristol a fait l'objet de relevés systématiques et continus depuis 1969. Les recherches sur le crabe royal bleu (*P. platypus*) ont été amorcées il y a moins longtemps, mais ses populations font l'objet de relevés de routine depuis 1974. Les estimations de populations et les informations biologiques obtenues par inventaire au chalut sont utilisées de pair avec les statistiques des pêches pour la gestion de ces deux espèces. L'auteur présente des méthodes permettant d'intégrer les données de relevés et de pêche, d'interpréter l'information ainsi obtenue et de l'appliquer à la gestion des pêches.

Les données de relevés et de pêche indiquent d'importantes fluctuations de l'abondance chez les deux espèces. L'abondance maximale du crabe royal exploitable commercialement dans la baie Bristol qui était estimée en 1979 à 46,6 millions d'individus de 2,9 kg de poids moyen avait chuté à 1,5 million d'individus en 1983, quand l'on a mis fin à la pêche. Les données des pêches corroborent les données des relevés et indiquent d'importantes fluctuations de l'abondance du crabe royal au cours des 30 dernières années. Les stocks du crabe royal bleu, qui ont aussi chuté depuis 1979, présentent des fluctuations atteignant environ un ordre de grandeur. Les fluctuations de l'abondance et les déclins récemment notés se sont produits en dépit de l'application de politiques de gestion visant à favoriser la stabilité, et les taux d'exploitation estimés n'ont jamais dépassé 60 % des mâles de la taille légale et au plus 10 % de la population de la baie Bristol. L'auteur attribue la diminution d'abondance aux effets réunis de l'importante mortalité naturelle et de la variabilité de la vigueur des classes annuelles plutôt qu'à l'insuffisance des mesures de gestion.

Introduction

Of the three commercially exploited species of king crabs in the eastern Bering Sea, red king crab (*Paralithodes camtschatica*) have been most important, followed by blue king crab (*P. platypus*) and golden (or brown) king crab (*Lithodes aequispina*). Over the last decade, eastern Bering Sea king crabs have supported some of the most profitable fisheries in North Pacific waters. Recent drastic declines in abundance of king crab stocks caused major dislocations in fishing and related industries, and therefore raised serious questions as to the adequacy of present methods of assessment and management. In describing the assessment and management of the three most important eastern Bering Sea stocks, I will concentrate on events within the past 10 yr but will draw on earlier history (Otto 1981) to illustrate trends. Finally, I will comment on the probable causes of population declines and implications for management.

Combined landings of Bristol Bay red king crab, Pribilof Islands blue king crab and St. Matthew Island blue king crab made up 99% of total eastern Bering Sea king crab landings from 1953 through 1983 (Table 1). Annual National Marine Fisheries Service (NMFS) trawl surveys have covered the ranges of each of these stocks for 6 or more years. Other stocks have been surveyed intermittently or partially. These three stocks were chosen for this paper because of the consistency of assessment data on them and their importance to the fishing industry.

TABLE 1. Historical landings of king crabs in the eastern Bering Sea (10^{-3}t, Bristol Bay red king crab, Pribilof and St. Matthew Islands blue king crab)[a].

Year	Bristol Bay		Pribilof Islands[b]		Saint Matthew Island	Other[c]	Total
	U.S.	Total	U.S.	Total			
1953	0.907	6.013	—	—	—	—	6.013
1954	1.056	4.724	—	—	—	—	4.724
1955	0.852	4.795	—	—	—	—	4.795
1956	0.860	4.629	—	—	—	—	4.629
1957	0.267	4.144	—	—	—	—	4.144
1958	0.003	3.694	—	—	—	—	3.694
1959	—	5.263	—	—	—	—	5.263
1960	0.271	11.435	—	—	—	—	11.435
1961	0.208	18.535	—	—	—	—	18.535
1962	0.034	24.195	—	—	—	—	24.195
1963	0.339	26.045	—	—	—	—	26.045
1964	0.413	29.024	—	—	—	—	29.024
1965	0.799	19.580	—	—	—	—	19.580
1966	0.452	19.498	—	0.912	—	—	20.410
1967	1.407	15.066	—	1.095	—	—	16.162
1968	3.940	15.772	—	0.725	—	—	16.496
1969	4.719	8.634	—	2.487	—	—	11.120
1970	3.882	9.166	—	0.582	—	—	9.747
1971	5.894	8.143	—	0.558	—	—	8.701
1972	9.863	11.868	—	0.136	—	—	12.004
1973	12.208	13.347	0.579	0.600	—	—	13.946
1974	19.172	22.797	3.224	4.009	—	—	26.807
1975	23.281	23.281	1.104	1.104	—	—	24.385
1976	28.994	28.994	2.999	2.999	—	—	31.993
1977	31.737	31.737	2.929	2.929	0.546	0.235	35.446
1978	39.743	39.743	2.901	2.901	0.900	0.960	44.504
1979	48.910	48.910	2.719	2.719	0.096	1.330	53.055
1980	58.944	58.944	4.976	4.976	0.100	0.956	64.976
1981	15.237	15.237	4.119	4.119	2.099	1.237	22.692
1982	1.361	1.361	1.998	1.998	3.831	0.436	7.626
1983	0.000	0.000	0.995	0.995	4.288	0.598	5.881
Totals:	315.754	534.573	28.543	35.843	11.859	5.752	588.028
Percentage	53.697	90.910	4.854	6.096	2.017	0.978	

[a] Data: 1953–1974 (Otto 1981), 1975–1983 (Alaska Department of Fish and Game 1984; Powell et al. 1983), minor differences in totals due to rounding.

[b] May include small amounts of Pribilof Island red king crab until 1979.

[c] Entirely Norton Sound red king crab 1977–1979, mostly Norton Sound and Pribilof Islands red king crab in 1980–1982, catches were 28.1% Norton Sound red king crab, 3.4% St. Lawrence Island blue king crab, 4.0% Pribilof Island red king crab and 64.4% golden king crab in 1983, when Bristol Bay was closed to commercial fishing.

Fishery Management

Exploitation of eastern Bering Sea king crabs began in 1930 with exploratory fishing by Japan (Harrison et al. 1942; Miyahara 1954). Japanese vessels had processed about 8.6 million red king crab by 1939 when the fishery was suspended. The United States conducted an exploratory cruise in 1940 (Harrison et al. 1942) and again in 1947 (King 1949, Ellson et al. 1949). By 1949 all major stocks of red and blue king crab in the eastern Bering Sea had been discovered. United States trawlers operated in the Bering Sea from 1949 to 1959, Japanese motherships (with tangle-net catcher boats) reentered the fishery in 1953 and similar Soviet operations began in 1959. The multinational phase of the fishery continued through 1974 when the Japanese left the fishery as a result of bilateral negotiations with the United States. In 1977, foreign fishing for king crabs within the U.S. 200-mile (370-km) zone became illegal under regulations implementing the Magnuson Fisheries Conservation and Management Act. From 1975 onward, eastern Bering Sea king crab fisheries have been characterized by expansion to new grounds, increased capitalization and phenomenal increases in annual catches followed by catastrophic declines.

Alaskan shellfish regulations (Alaska Department of Fish and Game, 1983) recognize seven stocks of king crabs in the eastern Bering Sea (Fig. 1). Ranked in order of importance (Table 1), these are: Bristol Bay red king crab (Statistical Area T), Pribilof Islands blue king crab (Pribilof District of Area Q), St. Matthew Island blue king crab (St. Matthew Section), Norton Sound red king

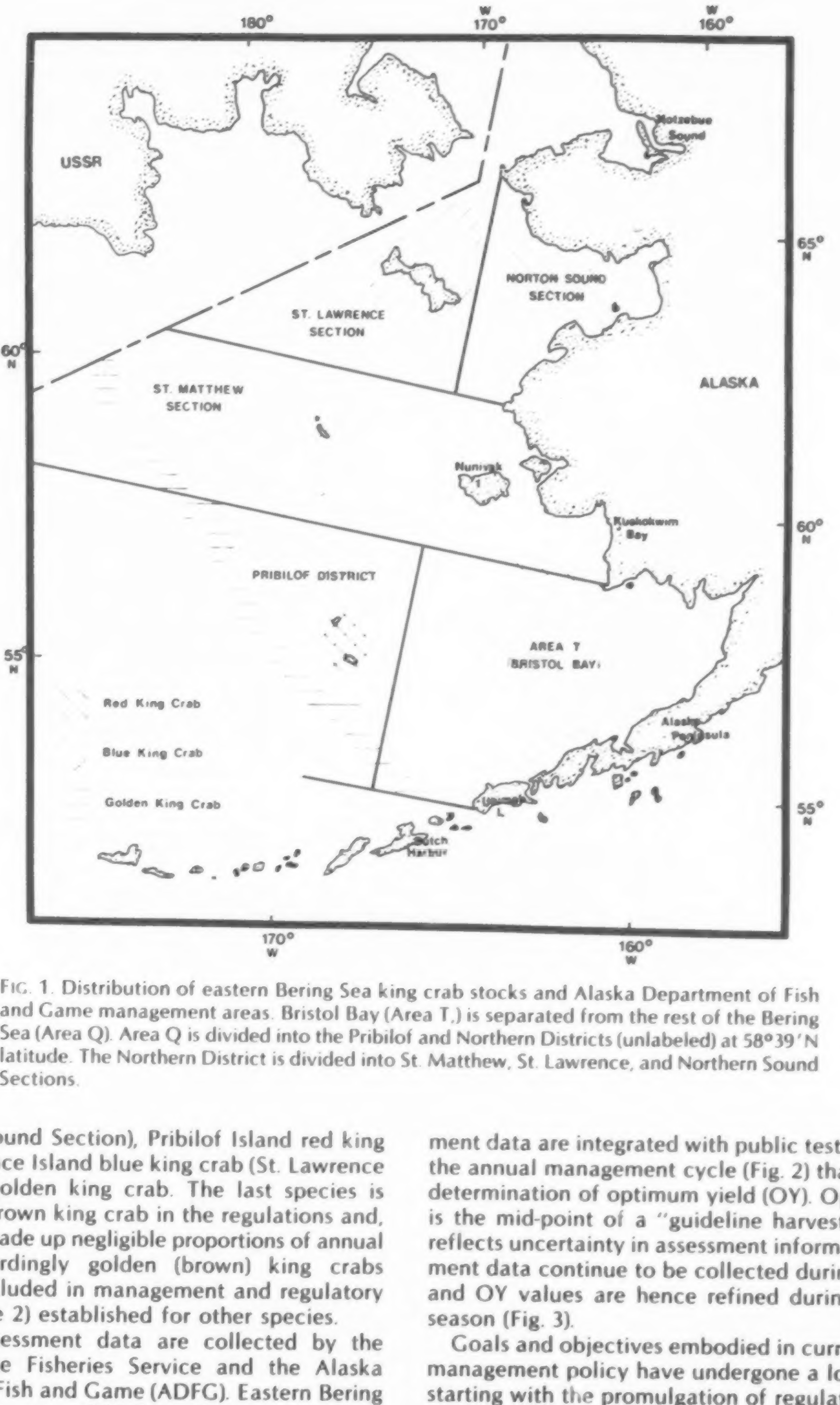

180°
W 170°
W 160°
USSR
Kotzebue Sound
65° N
NORTON SOUND SECTION
ST. LAWRENCE SECTION
60° N
ST. MATTHEW SECTION
ALASKA
Nunivak I
Kuskokwim Bay
60° N
PRIBILOF DISTRICT
AREA T (BRISTOL BAY)
55° N
Red King Crab
Blue King Crab
Golden King Crab
Alaska Peninsula
Unimak I.
55° N
Dutch Harbor
170° W
160° W

FIG. 1. Distribution of eastern Bering Sea king crab stocks and Alaska Department of Fish and Game management areas. Bristol Bay (Area T,) is separated from the rest of the Bering Sea (Area Q). Area Q is divided into the Pribilof and Northern Districts (unlabeled) at 58°39′N latitude. The Northern District is divided into St. Matthew, St. Lawrence, and Northern Sound Sections.

crab (Norton Sound Section), Pribilof Island red king crab, St. Lawrence Island blue king crab (St. Lawrence Section), and golden king crab. The last species is referred to as brown king crab in the regulations and, until recently, made up negligible proportions of annual landings. Accordingly golden (brown) king crabs were simply included in management and regulatory measures (Table 2) established for other species.

Resource assessment data are collected by the National Marine Fisheries Service and the Alaska Department of Fish and Game (ADFG). Eastern Bering Sea resource surveys and biological research are carried out primarily by NMFS. Monitoring of fishery performance and collection of biological data from landings are carried out by ADFG. Data collected by the two agencies provide independent measures of stock abundance, distribution and condition that are combined to provide an assessment of each stock. Assessment data are integrated with public testimony during the annual management cycle (Fig. 2) that results in a determination of optimum yield (OY). Optimum yield is the mid-point of a "guideline harvest range" that reflects uncertainty in assessment information. Assessment data continue to be collected during the fishery and OY values are hence refined during the fishing season (Fig. 3).

Goals and objectives embodied in current king crab management policy have undergone a long evolution starting with the promulgation of regulations in 1941. These early regulations included a size limit on male crab, a prohibition against landing females or soft-shelled crab and a requirement for reporting landings. Documentation of the reasoning behind these regulations is not available, but from later documentation, I assume that protecting reproductive potential, preventing waste, maintaining product quality and

TABLE 2. Comparison of regulations imposed on major eastern Bering Sea commercial crab fisheries with those in other Alaskan waters.[a]

Regulation	Bristol Bay Red King Crab	Pribilof Islands Blue King Crab	St. Matthew Is. Blue King Crab	Other Alaskan King Crab
Legal carapace width[b]	165 mm	165 mm	140 mm	121 mm (Norton Sound) 178 mm (Kodiak, etc.)
Season[c]	10/1 - 4/15	10/1 - 4/15	9/1 - 9/22	Open: 8/1 (Norton Sound) 11/10 (Adak)
Pot limit	None	None	None	100 Pots Per vessel (Kodiak, etc.)
Vessel registration[d]	Exclusive	Non-exclusive	Non-exclusive	Super-exclusive (Cook Inlet)
Harvest guideline[e]	Variable	Variable	Variable	90 to 227 metric tons (Southeastern)
Gear	Pots only	Pots only	Pots only	Pots, ringnets, scuba
Gear storage	(1) Depths <48 m (1) In quadrangle 57°N-58° 164°W-165°W	No storage in area 6/1-8/31, else Depths <48 m	(1) Depths <48 m (2) In quadrangle 59°N-59.5°N, 164.5°W-171°W	No storage 7 days after season closure (Southeastern)

[a] Modified from ADFG (1984). Entries for other Alaskan fisheries include only those outside ranges given for eastern Bering Sea fisheries. Golden king crab regulations and those common to all Alaskan waters are excluded (see text).

[b] Bristol Bay and some other fisheries actually may have a second season with a larger size limit. Size limits in the second season range from 178 mm in Bristol Bay to 203 mm in Cook Inlet. A second season has occurred only once (1981).

[c] Seasons usually close earlier (see Fig. 3) but must close by 4/15 in all Alaskan waters. Bering Sea seasons have been less than 90 d from 1975 onward.

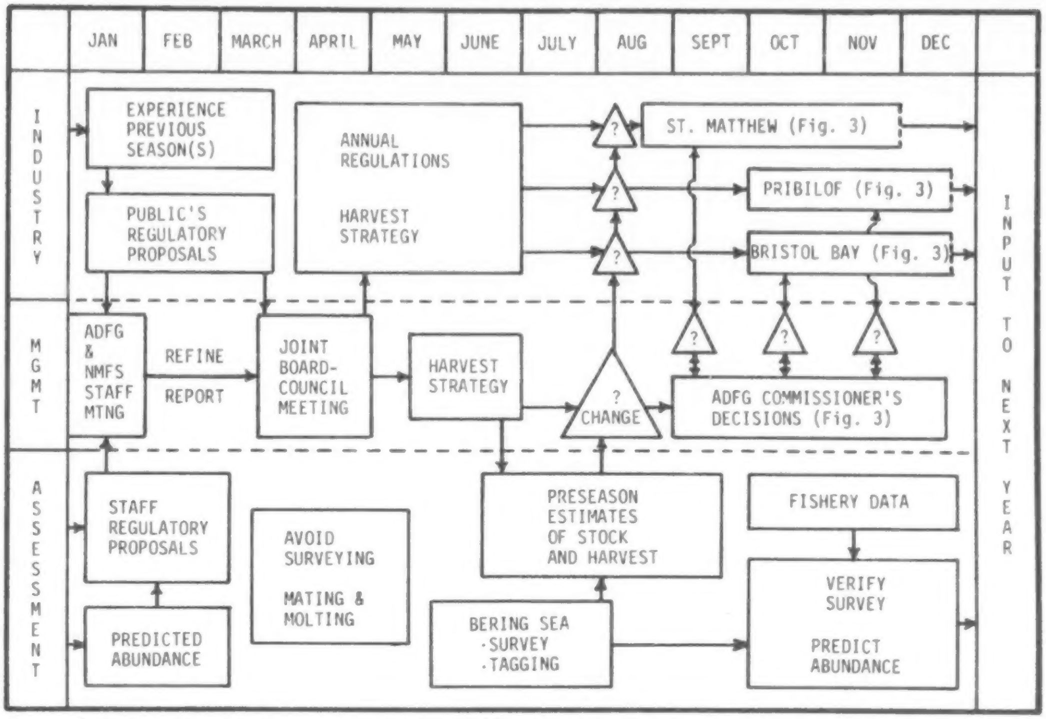
[d] Vessels registered in a super-exclusive area may not fish for king crab in any other area during the registration year. Vessels registered in exclusive areas may not fish in another exclusive area or in a super-exclusive area but may register for an unlimited number of non-exclusive areas. Vessels registered for a non-exclusive area may register for one exclusive area.

[e] Guideline harvest levels are quotas expressed as a range.

optimizing size at harvest were initial goals. Prohibition against landing soft-shelled crab later became a legal season regulation that prohibited fishing during molting or mating periods (March to May) and allowed newly molted crabs a growth period during which the amount of meat obtained from a given size of crab increased greatly. Prohibitions against use of trawls and tangle nets (a type of bottom gill net) were instituted to reduce handling mortality of females and sublegal males. Management areas were defined that recognized the existence of, and differences between, stocks in Alaskan waters. Regulatory measures serving initial goals were in place for all areas by 1969 and continue to be enforced. This set of goals and regulations is frequently referred to as "size–sex–season" management.

Initial management goals were augmented during the 1970's by goals intended to promote biological and economic stability. In the period between 1966 and 1970, landings of Alaska king crabs fell from 81 702 to 31 233 metric tonnes (t). Declines in the Kodiak area were particularly severe and landings fell from a peak of 42 834 t in the 1965–1966 season to 5 434 t in 1970. These developments resulted in the perception that management measures were inadequate, and management goals emphasizing stability in the fisheries were adopted. Quotas were imposed on fisheries in each management area. It was also recognized that drastic declines in landings were detrimental to local communities and a system of "exclusive" area registration was implemented to protect local fleets. A vessel registered in an exclusive area may not fish in another exclusive area during any given year. This provided indirect effort control. Pot limits are another form of effort control that relate to maintaining stability and protecting local industry.

The goals of management and regulation have not changed in any fundamental sense since they were discussed by Miller (1976) in relation to those in other North American crab fisheries. It is clear from Miller's (1976) work, that regulations imposed on king crab fish-


JAN
FEB
MARCH
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MAY
JUNE
JULY
AUG
SEPT
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DEC
INDUSTRY
MGMT
ASSESSMENT
INPUT TO NEXT YEAR
EXPERIENCE PREVIOUS SEASON(S)
PUBLIC'S REGULATORY PROPOSALS
ANNUAL REGULATIONS
HARVEST STRATEGY
?
ST. MATTHEW (Fig. 3)
PRIBILOF (Fig. 3)
BRISTOL BAY (Fig. 3)
ADFG & NMFS STAFF MTNG
REFINE
REPORT
JOINT BOARD-COUNCIL MEETING
HARVEST STRATEGY
? CHANGE
ADFG COMMISSIONER'S DECISIONS (Fig. 3)
STAFF REGULATORY PROPOSALS
PREDICTED ABUNDANCE
AVOID SURVEYING
MATING & MOLTING
PRESEASON ESTIMATES OF STOCK AND HARVEST
BERING SEA
·SURVEY
·TAGGING
FISHERY DATA
VERIFY SURVEY
PREDICT ABUNDANCE

FIG. 2. Annual cycle of management decision making for king crab stocks and its interaction with fisheries and resource assessment (modified from North Pacific Fishery Management Council 1984).

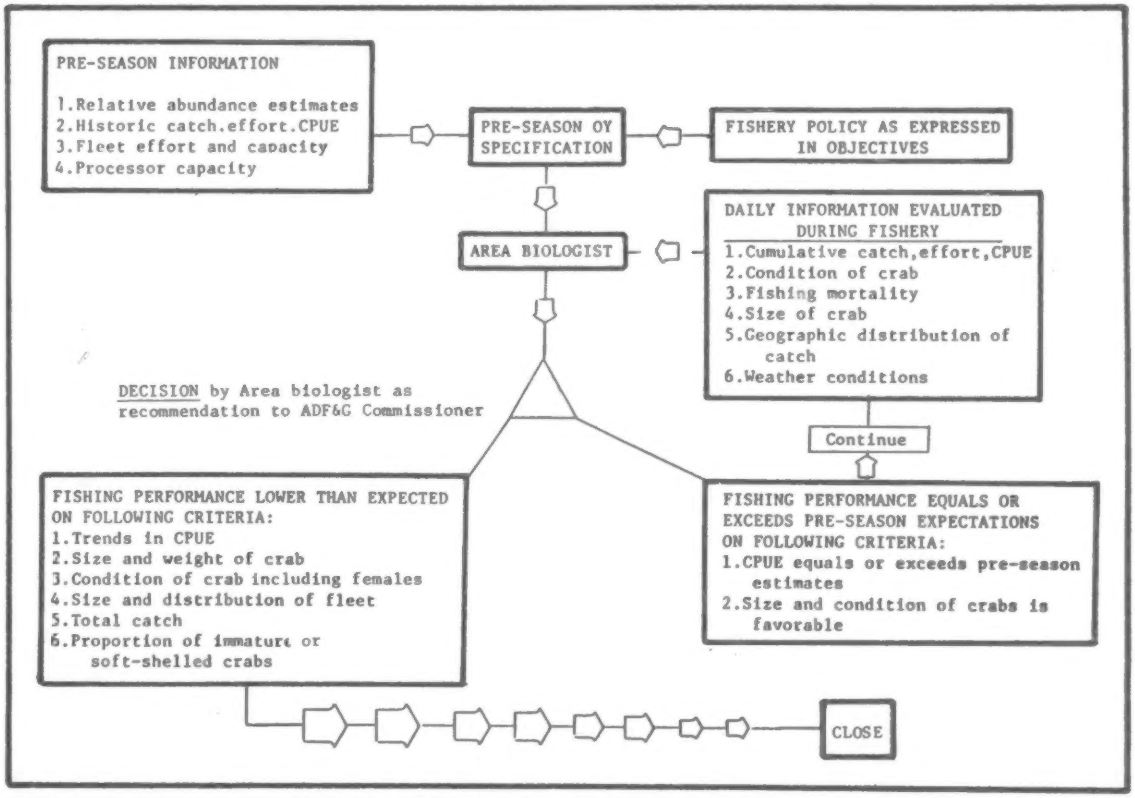

PRE-SEASON INFORMATION
1.Relative abundance estimates
2.Historic catch.effort.CPUE
3.Fleet effort and capacity
4.Processor capacity
PRE-SEASON OY SPECIFICATION
FISHERY POLICY AS EXPRESSED IN OBJECTIVES
AREA BIOLOGIST
DAILY INFORMATION EVALUATED DURING FISHERY
1.Cumulative catch,effort,CPUE
2.Condition of crab
3.Fishing mortality
4.Size of crab
5.Geographic distribution of catch
6.Weather conditions
DECISION by Area biologist as recommendation to ADF&G Commissioner
Continue
FISHING PERFORMANCE LOWER THAN EXPECTED ON FOLLOWING CRITERIA:
1.Trends in CPUE
2.Size and weight of crab
3.Condition of crab including females
4.Size and distribution of fleet
5.Total catch
6.Proportion of immature or soft-shelled crabs
FISHING PERFORMANCE EQUALS OR EXCEEDS PRE-SEASON EXPECTATIONS ON FOLLOWING CRITERIA:
1.CPUE equals or exceeds pre-season estimates
2.Size and condition of crabs is favorable
CLOSE

FIG. 3. In-season management decision making by Alaska Department of Fish and Game (ADFG) based on preseason specification of optimum yield (OY). Cycle at right continues until OY is reached. Area Management Biologists may issue field orders closing fisheries but final decisions are made by the Commissioner or his designee. Modified from North Pacific Fishery Management Council (1984).

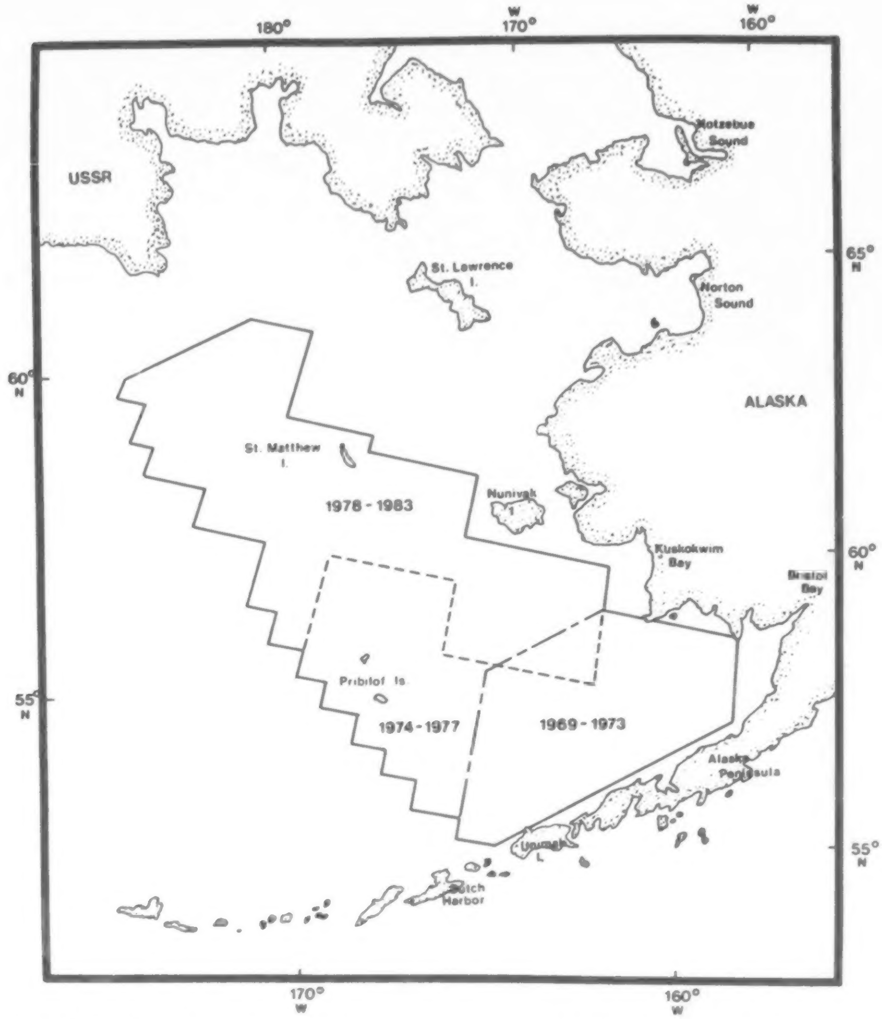


FIG. 4 Generalized areas surveyed by the National Marine Fisheries Service trawl survey in various years. Actual annual areas differ slightly from year to year.

eries are as, or more, restrictive than those on other North American crab fisheries and that they have allocative (economic) effects. The allocative aspects of Alaskan regulations are not always clear from their stated purposes (Katz and Bledsoe 1977). A Federal management plan has been developed (North Pacific Fishery Management Council (NPFMC) 1984) but not implemented. This plan incorporates all of the management measures described here and also includes various social, economic and administrative goals. I will not discuss these latter goals because they are not yet implemented, but it is important to note that biological aspects of king crab management are unlikely to change in the near future.

Assessment Data

A standard trawl survey to monitor distribution and abundance of king crabs has been conducted from 1969 to the present. Prior to 1969, trawl surveys were either intermittent or failed to cover the geographic range of any single stock. Areas covered by the survey (Fig. 4) have changed over time as budgets allowed and changes in fisheries warranted. Until 1974 the survey was directed at assessing Bristol Bay red king crab. Pribilof Islands blue king crab were added in 1974 and St. Matthew Island blue king crab were added in 1978.

The survey area in any given year is divided into 20 nautical mile (37.1 km) squares. Trawl stations usually are at the centers of squares and have consisted of either one-hour (1969–1976) or half-hour (1977–1983) tows. Trawl duration and gear comparison studies in 1977 showed no significant differences in apparent density of crabs between one-hour and half-hour tows and led to shorter tows in the interest of efficiency (Otto et al. 1978). Sampling is frequently augmented by making tows at the corners of squares or at random locations within them. Extra tows are used for specialized studies (e.g. gear comparison) or in an attempt to increase precision. Since blue king crabs near the Pribilof and St. Matthew Islands occupy relatively small areas, sampling is routinely augmented in these areas.

TABLE 3. Summary statistics for eastern Bering Sea crab fisheries as collected by the Alaska Department of Fish and Game[a]

Year	Vessels	Number of trips	Number of crab	Catch (10^3 t)	Pots lifted	CPUE	Avg Wt.	Avg Length
				Bristol Bay red crab				
1966	9	15	140 554	0.45	2 720	52	3.2	NA
1967	20	61	397 307	1.41	10 621	37	3.5	155.0
1968	59	261	1 278 592	3.94	47 496	27	3.1	NA
1969	65	377	1 749 022	4.72	98 426	18	2.7	143.8
1970	51	309	1 682 591	3.88	96 658	17	2.3	144.5
1971	52	394	2 404 681	5.89	118 522	20	2.4	144.9
1972	64	611	3 994 356	9.86	205 045	20	2.4	144.6
1973	67	454	5 000 383	12.20	200 909	25	2.5	145.5
1974	108	599	7 653 944	19.17	211 918	36	2.5	144.2
1975	102	592	8 745 294	23.28	205 096	43	2.6	145.8
1976	141	984	10 603 367	28.99	321 010	33	2.7	148.4
1977	130	1 020	11 733 101	31.74	451 273	26	2.7	147.9
1978	162	926	14 745 709	39.74	406 165	36	2.6	147.0
1979	236	889	16 808 605	48.91	315 226	53	2.9	152.3
1980	236	1 251	20 845 350	58.94	567 292	37	2.8	151.1
1981	177	1 026	5 307 947	15.23	542 250	10	2.9	151.0
1982	90	255	541 006	1.36	141 656	4	2.5	145.2
1983			SEASON NOT OPENED TO COMMERCIAL EXPLOITATION					
				Pribilof Islands blue king crab				
1973	8	13	174 420	0.58	6 814	26	3.3	NA
1974	70	101	908 072	3.22	45 518	20	3.5	157.8
1975	20	54	314 931	1.10	16 297	19	3.5	159.1
1976	47	113	855 505	2.10	71 738	12	3.5	158.1
1977	34	104	807 092	2.93	106 983	8	3.6	158.9
1978	58	154	797 364	2.90	101 117	8	3.7	159.3
1979	46	115	815 557	2.71	83 527	9	3.7	155.9
1980	110	258	1 497 101	4.97	167 684	9	[illegible]	155.7
1981	99	312	1 202 499	4.11	176 168	7	[illegible]	159.2
1982	122	281	587 908	2.00	127 728	5	3.5	159.8
1983	126	221	276 364	0.99	86 428	3	3.9	159.9
				St. Matthew Island blue king crab				
1977	10	24	281 665	0.5	17 370	16	2.0	130.4
1978	22	70	436 126	0.90	43 754	9	2.0	132.2
1979	18	25	52 966	0.10	9 877	5	1.8	128.8
1980	2	2	46 906	0.10	2 316	20	2.1	NA
1981	31	119	1 045 619	2.10	58 550	18	2.0	NA
1982	96	269	1 935 886	3.83	165 618	12	2.1	135.1
1983	164	235	1 931 990	4.29	133 944	14	2.2	137.2

[a] Modified from ADFG (1983). CPUE is crab per pot lift, avg wt. is in kilograms and length in millimetres. Catch data include crab that died in vessel holds ("dead loss"); landings are slightly less. Average weight computed from reported catch ("fish ticket" data). Average length determined by sampling of landings with sample sizes ranging from 9 723 to 34 529 for Bristol Bay, 1 117 to 5 905 for the Pribilof Islands, and 1 119 to 4 635 for St. Matthew Island.

All tows have been made during daylight hours throughout the history of the survey. Tows where the trawl was fishing properly and was not torn by objects on the bottom are judged as successful. Catches from all successful tows enter into computations of abundance. More detailed descriptions of survey patterns are contained in International North Pacific Fisheries Commission Annual Reports (e.g. Otto et al. 1984).

Trawls used in the annual survey are designed to insure contact between the footrope and the bottom. Footropes are about 30% longer than the headropes and are weighted with chain. The foot rope scours the bottom and various benthic molluscs are frequently taken. A "400 mesh eastern" otter trawl was the standard gear from 1968 through 1980. During 1981 one vessel used a larger but similar trawl (designated 83–112), while the other used the 400 mesh eastern. Side by side towing between the two vessels showed no significant differences in catch rates (crab per unit area) and the larger trawl was adopted as the standard in subsequent years (Otto et al. 1983). This change accommodated increased size of vessels used during recent surveys because they had difficulty in keeping the smaller trawl on bottom. Construction, rigging and mensuration characteristics of the two trawls are described by Wathne (1977).

The survey was conducted by a single vessel from 1969 through 1977 and by several (usually two) vessels thereafter to accommodate larger survey areas. One of the vessels used is owned by the Federal government (National Oceanic and Atmospheric Administration) and the others are chartered. The Federal vessel provides a standard of comparison from year to year. Comparisons of fishing power between vessels have been

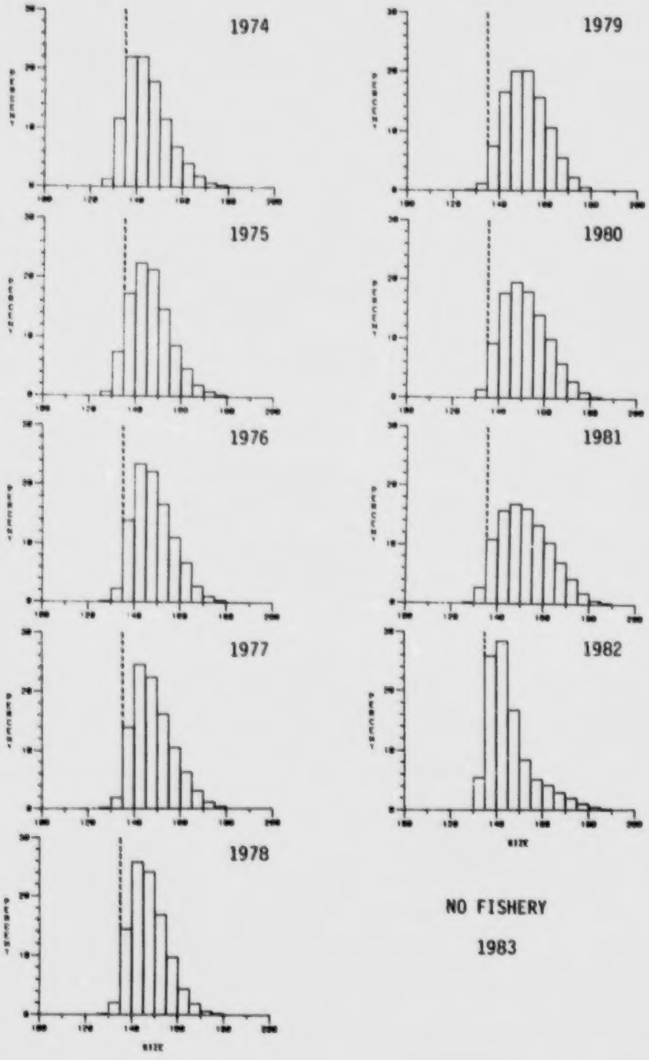


FIG. 5. Carapace length-frequency data from Alaska Department of Fish and Game samples from commercial catches of Bristol Bay red king crab. Dashed lines show legal size. Percentages are derived from sample sizes ranging from 9 723 in 1982 to 34 529 in 1980.

made each year either through side by side towing or by having each vessel occupy stations in alternate north-south columns of squares and later comparing mean catch rates. Statistically significant differences in catch rates of red king crab between vessels have seldom occurred, and were almost always attributable to number of tows made in areas of relatively high population density by one vessel as opposed to another. Because of their limited distribution, it has not been possible to judge the relative fishing powers of various vessels with respect to blue king crab and they have been assumed constant.

The catch from each tow is brought on deck and all crabs are removed. Crabs are then sorted by species and sex. If the number of crabs of a given species-sex category is large (>200) subsampling is accomplished by grasping crabs of approximately the same size and discarding one (occasionally more) of them. For extremely large catches, this procedure may be repeated or the catch may be sampled by weight. Since only males may be taken in the fishery, subsampling of males is avoided in favor of subsampling females. Usually the entire catch must be processed within 2 or 3 h and sampling is adjusted accordingly. After subsampling, carapace lengths (mm) are measured and each crab is also categorized for relative shell age (0 = in process of molting, 1 = soft, 2 = new shell, 3 = old shell or more than 1 yr since molting, 4 or 5 = progressively older shells). Eggs clutches on female crab are examined and coded according to egg condition (eyed, uneyed or dead) and relative size (nearest 25% of a full clutch of eggs). Other measures may include individual weights (g), chela heights (mm), or meropodite lengths (mm). Linear dimensions are defined by Wallace et al. (1949).

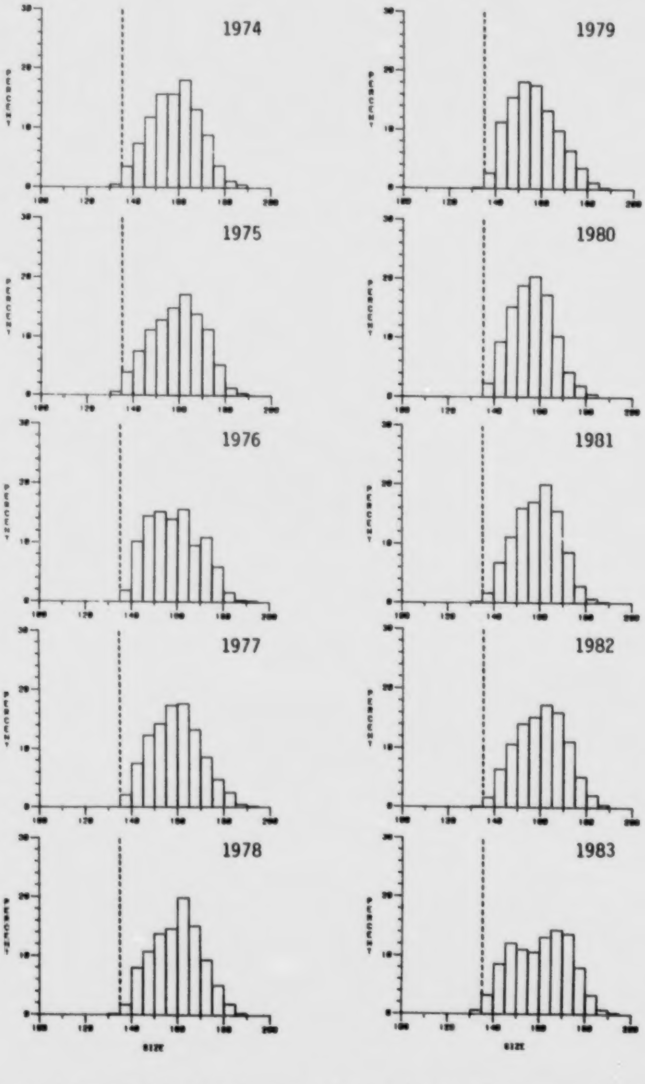


FIG. 6. Carapace length-frequency data from Alaska Department of Fish and Game samples from commercial catches of Pribilof Islands blue king crab. Dashed lines show legal size. Percentages are derived from sample sizes ranging from 1 117 in 1976 to 5 905 in 1983.

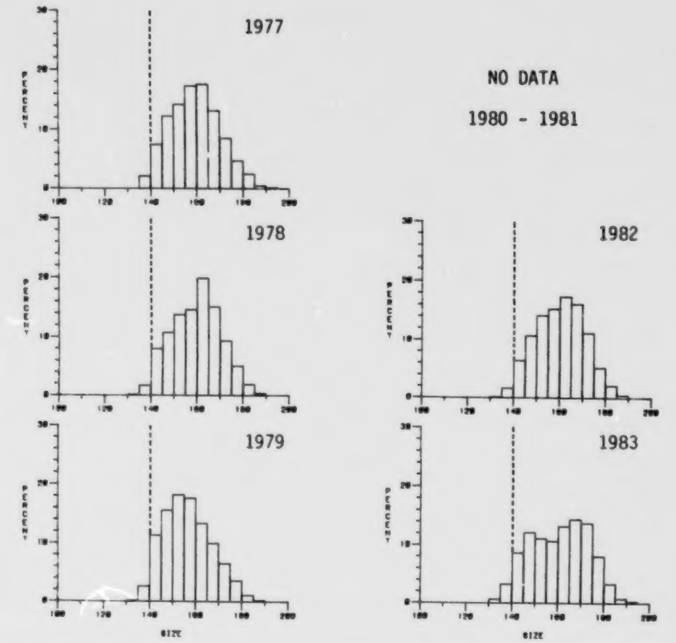


FIG. 7. Carapace length data from Alaska Department of Fish and Game samples from commercial catches of St. Matthew Island blue king crab. Dashed lines show legal size. Percentages are derived from sample sizes ranging from 1 119 in 1979 to 4 635 in 1983.

Due to variability in periodicity of molting and growth per molt, there is no precise way of knowing the age of a given king crab. Year-class modes are typically obscured over most of the size range that is encountered during surveys. Tagging studies have, hence, been essential to estimate growth and mortality rates. Tag returns from commercial fisheries have been analyzed to determine the probability of molting and to characterize incremental growth per molt. Descriptive models of growth based on data from tag returns (Webber and Miyahara 1962; Hoopes and Greenough 1970; Balsiger 1974; McCaughran and Powell 1977), along with estimates of mortality, provide a basis for predicting abundance from year to year. Analysis of tag return data by Balsiger (1974) provided the growth transition matrix and size specific natural mortality estimates for calculations described below.

King crabs are tagged with "spaghetti" or loop tags (Anon. 1954; Stevens 1955; Hayes 1963; Gray 1965) threaded through the isthmus in the membrane connecting the carapace to the first abdominal somite. These tags have a long history of use, apparently cause minimal mortality and are retained through molting. Bristol Bay red king crab have been tagged in various years since 1955 and most recently in 1981. Tagging of Pribilof Islands blue king crab was initiated in 1978 and followed by tagging in the St. Matthew Islands area in 1982 and 1983. Few tags have been returned from the latter two areas, however and insufficient data are available to characterize growth and mortality.

Data gathered by ADFG during port sampling and from reported landings ("fish tickets") allow estimation of size specific fishing mortality and provide measures of fishery performance that are used to verify abundance estimates from surveys. Almost all Bering Sea king crabs are landed at Dutch Harbor, Akutan, or floating processors located closer to the grounds (Port Moller, the Pribilofs or near St. Matthew Island). Biologists assigned to these locations gather a variety of fishery and biological data. For assessment purposes, measures of fishery performance (Table 3) and size frequency of removals (Fig. 5-7) are most useful. Data on condition of crabs (relative shell age, product recovery rates), numbers dead in vessel live tanks ("dead loss") and fishing conditions, however, are also essential to management decision making (Fig. 3).

Analysis of Assessment Data and Predictions of Stock Abundance

Although all above sources provide data for resource assessment including considerable life history information (Table 4), estimating and predicting abundance has been of primary importance. This has been necessary from the standpoint of annual decision making and because Bering Sea king crab stocks undergo substantial fluctuations in abundance (Fig. 8, Table 5). Size-frequency distributions (Fig. 9-11) show considerable year to year variation and indicate that differences in year-class strength are large (Incze et al 1986). As judged by catch per unit effort in the commercial fishery and survey estimates, the abundance of legal crab

TABLE 4. Comparative life-history data for red and blue king crabs in the eastern Bering Sea.[a]

Observation	Red king crab	Blue king crab
Habitat	All bottom types, early juveniles on rock or rubble, warmer waters	Closely associated with islands and rock or rubble (adult males may occur on smooth bottom), colder waters
Juveniles	Closely resemble adults in color and shape but spines more prominent, form hive shaped aggregations called pods	Differ from adults in body shape and coloration, carapace color ranges from white to tan or red (thought to be protective), spines less prominent than adults, not known to form pods
Growth	Adult males average 15 to 16 mm per molt. Molting frequency decreases with age	Adult males average 15–16 mm in Pribilofs, frequency not known, no data for St. Matthew Island
Feeding	Omnivorous (bivalves, echinoderms, fish, barnacles, crustaceans)	Presumed similar but not well described
Oviposition	Normally annual	Normally biennial
Fecundity (E)	$E = -247,400 + 3,319\ L$	$E = 241629 - 2632606 \exp(-.028023L)$
Female maturity	90 mm	96 mm (Pribilofs), 80 mm (St. Matthew)
Length vs weight (males)	$\ln W = -14.83 + 3.16 \ln L$	$\ln W = -8.02 + 3.175L$ (Pribilofs) $\ln W = -5.36 + 3.103L$ (St. Matthew)
Average landed weight	2.3 to 3.5 kg	3.5 to 3.6 kg (Pribilofs) 1.8 to 2.2 kg (St. Matthew)

[a] Data from various authors (see text) augmented by unpublished NMFS observations. Principal references for red king crab are Wallace et al. (1949), Haynes (1968), Balsiger (1974), Feder and Jewett (1981), Otto et al. (1980); those for blue king crab include Sasakawa (1973, 1975a, 1975b), Somerton and MacIntosh (1983a, 1983b), Otto et al. (1983).

may change by an order of magnitude within a period less than 5 yr. This situation has resulted in considerable reliance on annual abundance estimates and inseason fishery data collection for making management decisions. A predictive capability is also necessary, however, because of timing (Fig. 2) and to allow the fishing industry to make adjustments.

Data from the trawl survey were analyzed using the area-swept technique (Alverson and Pereyra 1969; Hoopes and Greenough 1970) and stratified random sampling techniques (Cochran 1963) to provide estimates of abundance for 1966 (Kirkwood and Hebard 1969), 1968 (Hoopes and Greenough 1970), 1969, 1970, and 1972 through to the present. Methods of computation described below have been constant since 1974. Estimates from prior years are comparable but derived from simple rather than stratified sampling. The observed density of crabs in a given size–sex group from a given trawl tow (D) is measured (ignoring subscripts) as,

$$D = n/farq,$$

where: n = number of males or females taken in a given 5 mm group;
f = fraction of crab sampled;
a = area swept by the trawl as estimated by the geodetic position at the beginning and end of the tow and the average effective width of the trawl (assumed 90% of average wing spread);
r = relative fishing power designated as 1.0 for the standard (usually government owned) vessel and as a ratio (usually also 1.0) for other vessels;
and, q = probability of capture given encounter (assumed to be 1.0 for king crabs).

I term D an observation of density because there is no statistical treatment given to inherent variability arising through subsampling. Densities of crab in the i^{th} 5 mm carapace length group from the j^{th} tow in the k^{th} stratum (see below) are combined in an annual abundance estimate (N) as,

$$N = \sum_{k=1}^{\ell} A_k \sum_{i=1}^{s} \overline{D}_{ik}$$

where:

A = to the area of the k^{th} stratum;

and $\overline{D}$ = to the average density of crab in the i^{th} size (sex) group averaged over $j = 1, n_k$ tows in a stratum.

In each year, the habitat area of each stock is delineated by plotting distribution of all sizes and sexes combined. This area is then stratified on the basis of density of large males and areal distribution of tows (sampling density). This procedure (Fig. 12) has been somewhat subjective and has varied slightly from year to year. Tows are grouped by grid squares if necessary and densities of legal males are plotted. If these densities are greater than the mean plus one standard error, squares are classified as "high" concentration. This step usually results in well defined but somewhat irregular areas that serve as nuclei for defining high concentration areas. If there is no geographic continuity to high concentration areas, stratification on the basis of crab density is abandoned. As a second step, high concentration nuclear areas are expanded by smoothing irregularities, filling in holes or constructing bridges between adjacent areas. This is done by: (1) including

TABLE 5. Annual abundance estimates (millions of crabs) for eastern Bering Sea king crabs from NMFS trawl surveys (Otto et al. 1984).

Size[b]	Males				Females			Grand total
	<110	110-134	>134	Total	<90	>89	Total	
				Bristol Bay red king crab[a]				
1969	41.0	20.3	9.8	71.1	18.3	28.5	46.8	117.9
1970	9.5	8.4	5.3	23.2	4.9	13.0	17.9	41.1
1972[c]	14.1	8.0	5.4	27.5	7.0	12.1	19.1	46.6
1973	50.0	25.9	10.8	86.7	24.8	76.8	101.6	188.3
1974	59.0	31.2	20.9	111.1	37.7	72.0	109.7	220.8
1975	84.9	31.7	21.0	137.6	70.8	58.9	129.7	267.3
1976	70.2	49.3	32.7	152.2	35.9	71.8	107.7	259.9
1977	80.2	63.9	37.6	181.7	33.5	150.1	183.6	365.3
1978	62.9	47.9	46.6	157.4	38.2	128.4	166.6	324.0
1979	48.1	37.2	43.9	129.2	45.1	110.9	156.0	285.2
1980	56.8	23.9	36.1	116.8	44.8	67.6	112.5	229.3
1981	56.6	18.4	11.3	86.3	36.3	67.3	103.6	189.9
1982	107.2	17.4	4.7	129.3	77.2	54.8	132.0	261.3
1983[d]	43.3	10.4	1.5	55.2	24.3	9.7	34.0	89.2
				Pribilof Islands blue king crab[e]				
1974	4.4	3.1	1.9	9.4	0.6	10.9	11.5	20.9
1975	4.1	8.0	7.5	19.6	0.0	8.8	8.8	28.4
1976	10.3	2.1	3.9	16.3	0.4	17.7	18.1	34.4
1977	3.2	2.2	9.4	14.8	2.2	17.5	19.7	34.5
1978	1.2	5.8	4.3	11.3	0.3	35.5	35.8	47.1
1979	6.4	1.5	4.6	12.5	5.2	2.9	8.1	20.6
1980	1.9	1.4	4.2	7.5	0.8	101.9	102.7[f]	110.2
1981	4.8	1.4	4.2	10.4	3.4	11.6	15.0	25.4
1982	1.2	0.7	2.2	4.1	0.7	8.6	9.3	13.4
1983	0.6	0.8	1.3	2.8	0.2	9.2	9.4	12.2

Size[b]	Males				Females			Grand total
	<105	105-119	>119	Total	<80	>79	Total	
				St. Matthew Island blue king crab[g]				
1978	5.6	2.4	1.8	9.8	0.8	0.4	1.2	11.0
1979	4.9	2.3	2.2	9.4	1.7	0.9	2.6	12.0
1980	3.4	2.2	2.5	8.1	0.8	2.2	3.0	11.1
1981	1.2	1.8	3.1	6.3	0.0	0.5	0.5	6.8
1982	3.2	2.6	6.8	12.5	0.4	0.7	1.1	13.7
1983	1.8	1.6	3.5	6.9	0.2	2.4	2.7	9.6

[a] These data include small numbers of Pribilof Island red king crab, 95% confidence interval half-widths ranged from: 10 to 24% for 110-134 mm males, 12 to 27% for larger males and 11 to 23% for large females, half-widths for smaller crab of both sexes are greater.

[b] Carapace length (mm); 135 mm carapace length corresponds to legal size of 165 mm carapace width: for Bristol Bay and Pribilof Islands fisheries, estimates for smallest size groups not reliable due to size selectivity of trawls employed and limited sampling in waters less than 50 m. Legal size in the St. Matthew Island fishery is 140 mm width which corresponds to 120 mm carapace length.

[c] Limited survey in 1971, not used for population estimate.

[d] 1983 data includes small numbers of crab from the Northern District (north of 58°39'N) due to changes in geographic distribution.

[e] Half-widths of 95% confidence intervals ranged from 33 to 86% for 110-134 mm males, 13 to 28% for larger males and 28 to 101% for large females; confidence intervals for smaller crab tend to be wider.

[f] Estimates for females and grand total considered unreliable in 1980.

[g] Categories reflect smaller average size in the Northern District; 80 mm is the median size at maturity for females. Half-widths of 95% confidence intervals ranged from 40 to 59% for 105-119 mm males, 19 to 47% for larger males and 63 to 108% for large females; confidence intervals for smaller crabs tend to be wider. Carapace length of 120 mm corresponds to legal size of 140 mm.

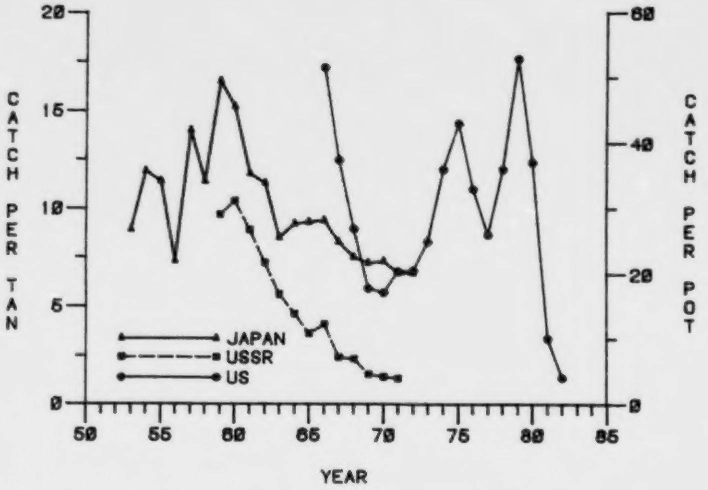


FIG. 8. Nominal catch per unit effort in the Bristol Bay red king crab fishery showing fluctuating abundance with major lows in 1970 and 1983 (fishery closed). Data for Japan and the USSR are for tangle net lifts (one tan is approximately 40 m of net). Data for the U.S. are in pot lifts (average dimensions of pots are 2.1 × 2.1 × 0.9 m).

"low" squares in the high category if four or more adjacent (including diagonals) squares are "high," and (2) by including other adjacent squares if "high" densities of males that are within one to two molting increments of legal size (e.g. 110 to 134 mm) are present. If there are well defined areas where sampling density exceeds one tow per grid square, the above steps are carried out separately in areas of "low" and "high" sampling density. In cases where the habitat areas overlap management area boundaries, stratification is carried out by management area (Fig. 1) as well. The above procedures result in a variable number of strata that are combined to calculate abundance.

Estimates of abundance are computed for each sex, each 5 mm size group ($N_{i..}$) and each stratum ($N_{..k}$ or N_{ik}). Estimates (N_{ik}) are then summed as appropriate for applications such as estimates of total legal stock or legal stock in a management area. Variances are computed as,

$$S^2 = \sum_{k=1}^{\ell} A_k^2 S_k^2$$

where: S is the standard deviation (or error) of the estimate in question,
and, S_k is the stratum variance.

This is the variance of a sum of variables assuming that they are statistically independent. This assumption is well applied for combinations of strata being summed by management area. Variances for estimates of abundance for various size groups (Table 5), however, are computed by summing variances of estimates by 5 mm group even though it may not be correct to consider estimates for adjacent 5 mm groups as statistically independent variables. Confidence intervals are taken as twice the standard errors of estimated abundances. For Bristol Bay red king crab samples, sizes are large (>50 tows per year) and it is reasonable to assume a normal distribution of errors around estimates of abundance. For blue king crab stocks, sample sizes are smaller and estimates of precision may be biased.

The 95% confidence interval for legal males is generally 15–20% for red king and only slightly larger for blue king crabs. Precision tends to decrease at either end of the size range (Fig. 13). In the case of largest males loss of precision is not important because very few crabs are involved. Precision of estimates for intermediate sized males is usually similar to that of legal males, while that for large females is about half as good. For most purposes, population estimates of crabs less than 90 mm are considered unreliable. For the smaller size groups, confidence intervals are wide due, in part, to their extremely patchy distribution and their invulnerability to the gear. Because smaller crabs of both species frequently inhabit untrawlable habitats, estimates of their abundance (and hence population totals) are inevitably low as well as imprecise.

Sampling power of the commercial fleet is much greater than that of the research vessels; however, commercial fishery data have some limitations concerning the segment of the population sampled, possible inaccuracies in reporting, and possible sampling bias related to size frequencies of landings at monitored and unmonitored processing sites. Detailed summaries of fishery data for the eastern Bering Sea are provided annually in Westward Region Shellfish Reports to the Alaska Board of Fisheries (e.g. ADFG 1984). Overall catch per unit effort and catch in the fishery each fall are correlated with survey-derived estimates as a measure of the survey's validity (Fig. 14 and 15). Leslie or DeLury methods (Ricker 1975) may also provide independent estimates of stock abundance that can be compared to survey estimates (Fig. 16). Unfortunately, seasons frequently are too short to use Leslie–DeLury methods. Finally, total catch is prorated by size fre-

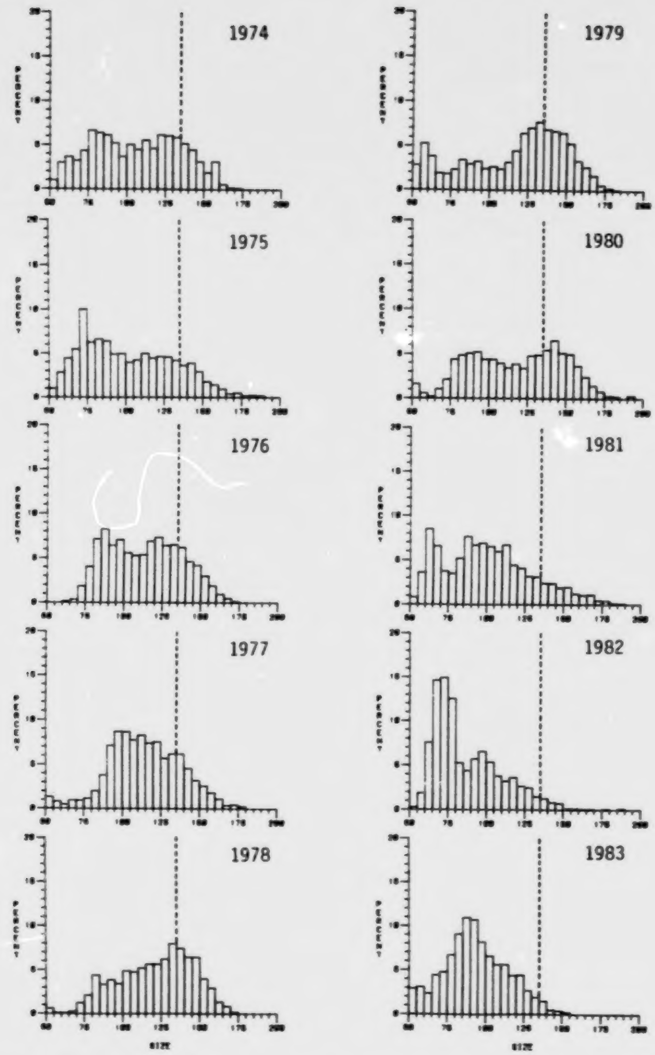


FIG. 9. Carapace length-frequency data from samples of male Bristol Bay red king crab taken during National Marine Fisheries Service trawl surveys. Dashed lines show legal size. Percentages are derived from population estimates per 5 mm carapace length group. Numbers of male crab caught ranged from 1 712 in 1983 to 7 656 in 1979.

quency distribution of crabs measured from landings to estimate harvest in each 5 mm group. These estimates are used to interpret differences in survey and fishery derived abundance estimates and in calculating size-specific fishing mortality rates.

Following each fishing season, survey estimates, fishery data, and estimates of growth and natural mortality are used to make projections of future abundance for male crabs. In the case of Bristol Bay red king crab, these calculations can be made on the basis of 5 mm size groups. Calculations of future abundance (Table 6) for red king crab are made for the following time periods from a given survey:

a) at the start of the fishing season immediately following the survey (omitted if less than one month),
b) following the fishing season (exploitation rates are evaluated at this point),
c) at the beginning of the molting period (February-March),
d) at the end of the molting period (May-June),
e) at the projected midpoint of the following year's survey, (FORCAST1 in Fig. 14).
f) at the projected opening date of the following season,
g) at subsequent times by applying size specific exploitation rates from one season (*b* above) and management targeted exploitation (Table 7) to estimates at time *f* (FORCAST2 in Fig. 14); and repeating steps *b–f*.

For blue king crab stocks, calculations are less

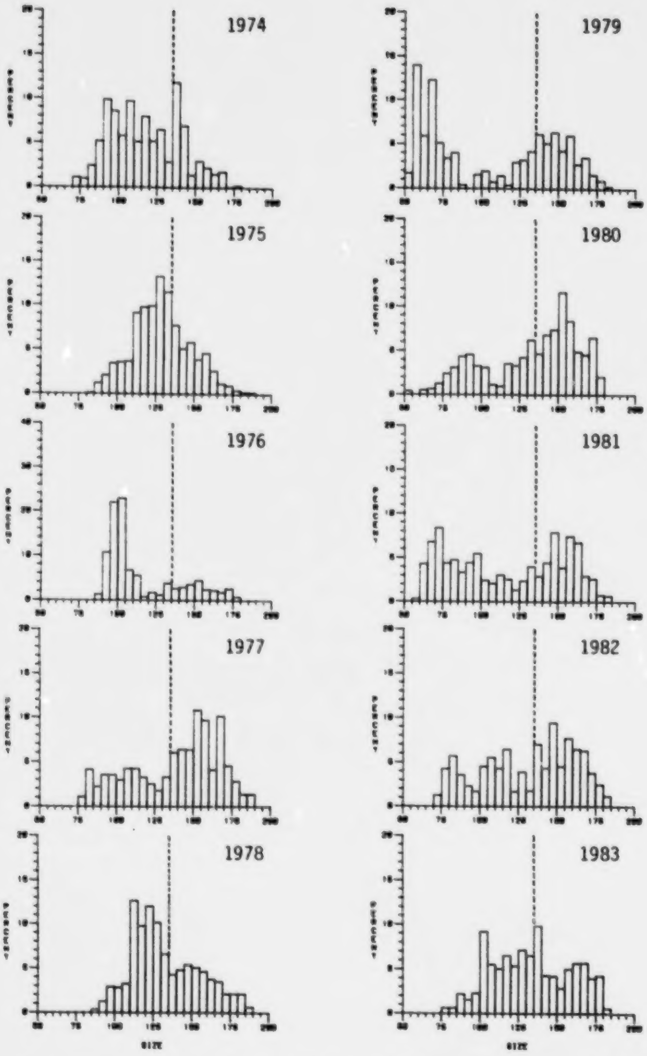


FIG. 10. Carapace length-frequency data from samples of male Pribilof Islands blue king crab taken during National Marine Fisheries Service trawl surveys. Dashed lines show legal size. Percentages are derived from population estimates per 5 mm carapace length group. Numbers of male crab caught ranged from 136 in 1983 to 859 in 1975.

detailed because larger size groups are used, growth and mortality are poorly known, and fishery data are less complete. Growth and mortality rates for red king crab of comparable size are applied to blue king crab because estimates of these parameters are not available for stocks of the latter species. For Pribilof Islands blue king crab we know average growth per molt of adult males (Otto et al. 1983) is almost identical to that for Bristol Bay red king crab (Table 4), but must assume that annual molting frequencies and natural mortality rates are also identical. For St. Matthew Island blue king crab, rates of growth and mortality are assumed to be similar to those of red king crab at comparable life stages. Projections for blue king crab are made only one year ahead and two size groups (one year prerecruit and legal) are used in the calculation. The pre-recruit size range is 120–134 mm for the Pribilof Islands and 105–119 mm for St. Matthew Island. Comparison of predicted abundance with other indices of abundance (Fig. 15) shows that assumptions are better met with Pribilof Islands than with St. Matthew Island blue king crabs.

Adequacy of Assessment

Assessment efforts are adequate only when management and industry believe in resulting estimates and are willing to act upon them. This is true even if estimates are extremely accurate. Overall, seasonal fishery data have tended to corroborate both population estimates

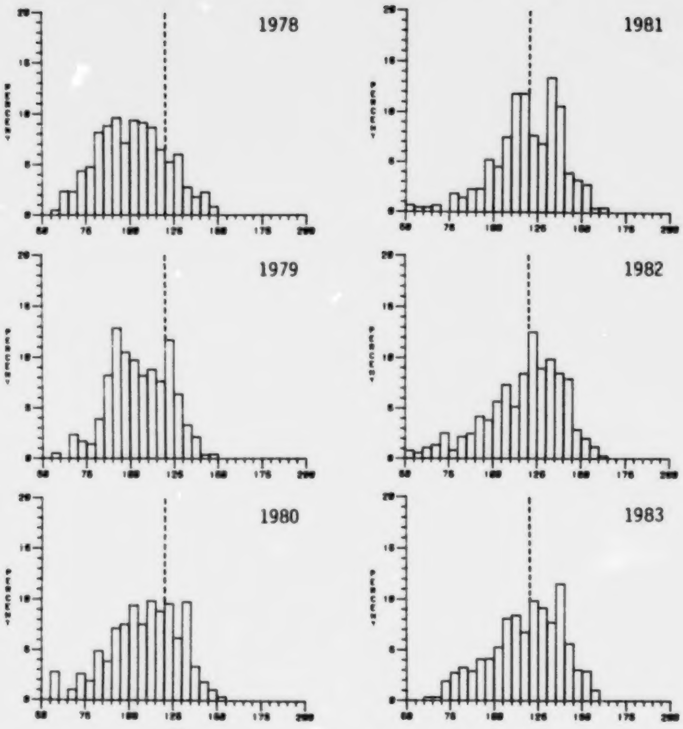
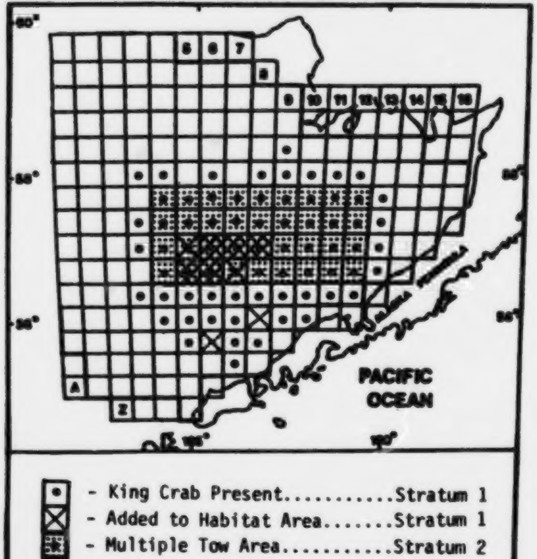


FIG. 11. Carapace length-frequency data from samples of male St. Matthew Island blue king crab taken during National Marine Fisheries Service trawl surveys. Dashed lines show legal size. Percentages are derived from population estimates per 5 mm size group. Numbers of male crab caught ranged from 218 in 1981 to 343 in 1982.


60°
58°
56°
5
6
7
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11
12
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14
15
16
A
Z
PACIFIC
OCEAN
165°
160°
- King Crab Present...........Stratum 1
- Added to Habitat Area.......Stratum 1
- Multiple Tow Area...........Stratum 2
- High Density Nucleus........Stratum 3
- Added to High Density.......Stratum 3

FIG. 12. A hypothetical stratification of survey data for Bristol Bay red king crab. Stratum one is low crab density — one tow per square, stratum 2 is low crab density — multiple tows per square, stratum 3 is high crab density — multiple tows per square. Stratum areas are the sum of areas for squares in each stratum. The example does not include the possibility of a high density — single tow stratum.

and predictions. Further, the comparability of survey estimates and predicted abundance with fishery performance has tended to improve with time (Fig. 14 and 15). In this regard, the system in place either appears to be meeting the needs of the current management regime (Bristol Bay, Pribilof Islands) or soon will meet them (St. Matthew Island). There is, however, a need for reasonably accurate forecasts that extend more than two years into the future. Since long term financing and planning are almost always necessary, the lack of enhanced predictive capability places a burden on industry.

A long history of biological research on Asian and North American stocks of red king crab provided considerable background information that was applied in Bristol Bay throughout the history of the fishery. Further, the historical dominance of this stock in eastern Bering Sea fisheries led to continuous research and assessment efforts. This stock is extremely amenable to trawl surveys because almost all of its habitat consists of smooth bottom and the habitat area is large enough to ensure adequate sample sizes during a large scale, multipurpose survey. Unfortunately, the precision of estimated abundance at sizes smaller than 100 mm (Fig. 13) is not comparable to that of 100–140 mm crabs. Legal size (165 mm width) corresponds to 135 mm length, and growth per molt of adult male crabs averages about 15 mm in length (Table 4). Estimates of abundance for prerecruits in the 100–134 mm size groups, then, can be used to provide relatively precise

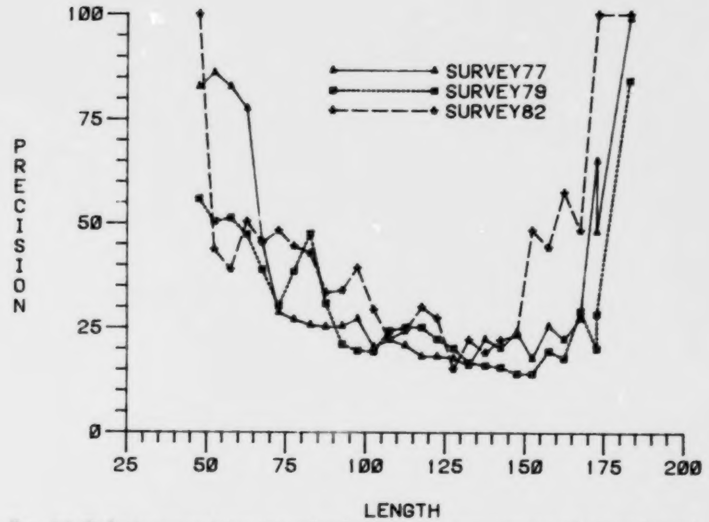

FIG. 13. Relative precision (standard error as a percentage of abundance) of estimated abundance by 5 mm carapace length groups for male Bristol Bay red king crab. Data for blue king crab stocks show a similar pattern but are less precise.

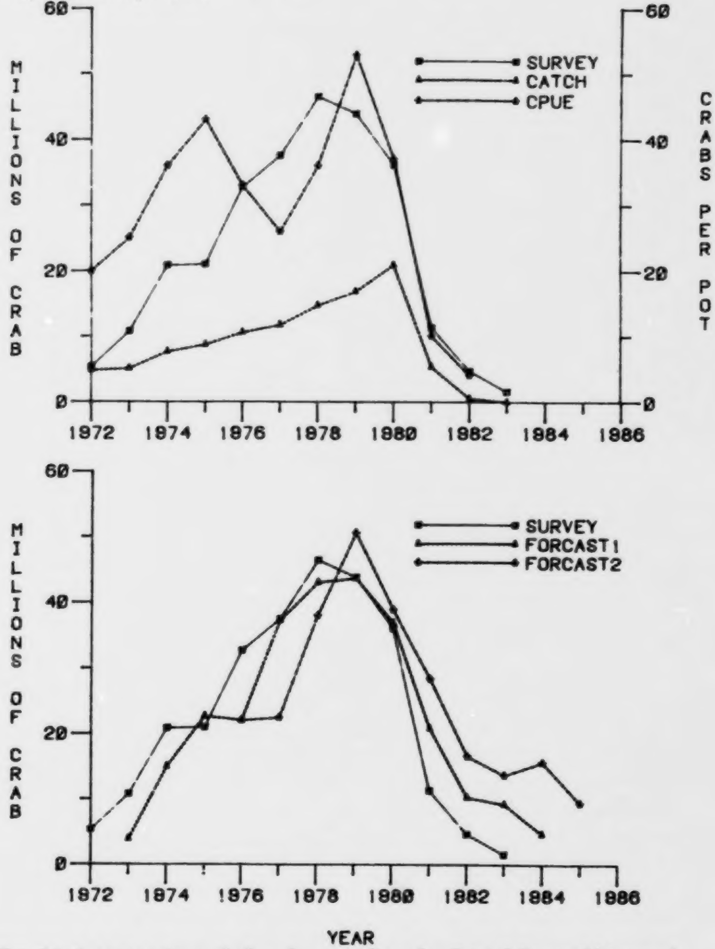

FIG. 14. A comparison of abundance indices for Bristol Bay red king crab. Top panel shows estimated abundance of legal males from the survey in comparison with nominal catch and catch per unit (pot lift) effort in the U.S. fishery. Bottom panel shows survey abundance in comparison with predicted abundance from surveys taken 1 (FORCAST1) and 2 (FORCAST2) yr previously (calculations per Table 6).

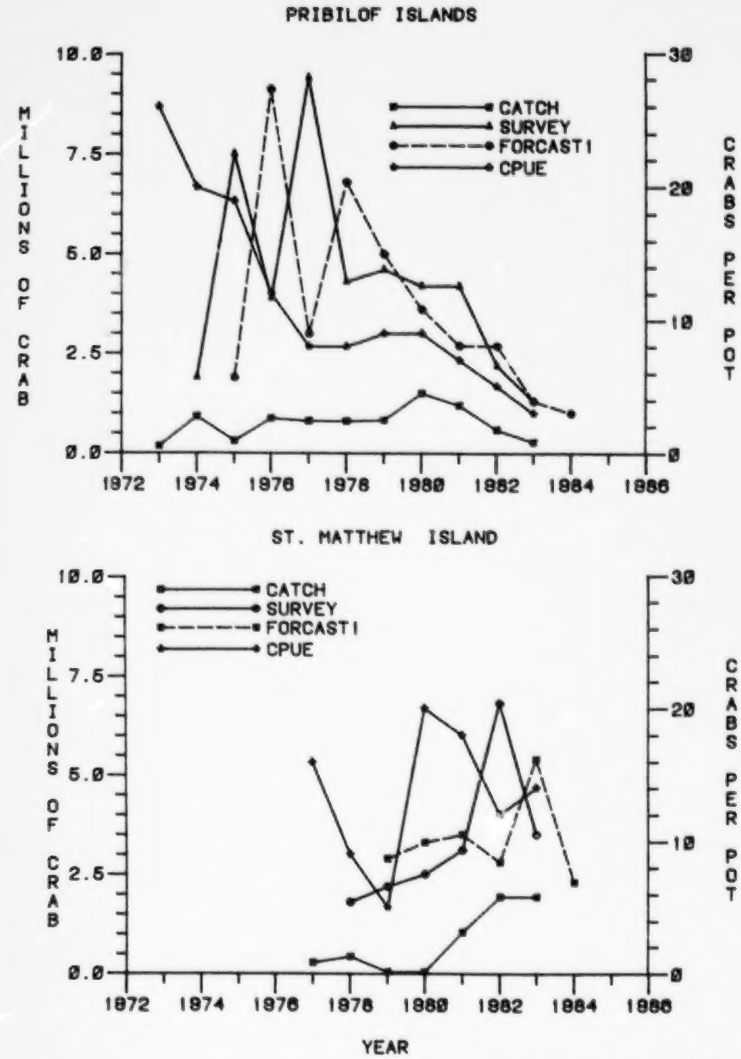

FIG. 15. A comparison of survey estimates of legal male abundance and one year forecasts (FORCAST1) with nominal catch and catch per unit effort for Pribilof Islands and St. Matthew Island blue king crab. Catch, estimates of legal stock (survey) and one year forecasts (FORCAST1) are in millions of crab; CPUE is crab per pot lift.

predictions of legal abundance for only about 2 yr. Better estimates of abundance for crab less than 100 mm would enhance predictive capability.

Comparisons of survey and fishery-based Leslie estimates of legal stock (Fig. 16) show that Leslie estimates are consistently smaller. While there are only 5 yr during which the two types of estimates may be compared, they illustrate the same trend in abundance and tend to be closer together in years when the catch was large relative to the survey estimate (Fig. 14). Differences between the two sets are largely explainable on the basis of lower exploitation rates on crab in the smaller legal size groups (compare Fig. 5 and 9) and by the fact that areas with sparse concentrations of legal crab are included in survey estimates but generally are not fished commercially.

Although the general correlation between survey estimated abundance of legal males and commercial CPUE is close, discrepancies still exist. Declining catch per unit effort from 1975 to 1977 coincided with increasing estimates of abundance (Fig. 14) raising doubts as to the accuracy of the latter. This anomaly might be partly explained by an influx of vessels into the fishery (Table 3) but subsequent influxes of comparable magnitude did not have such an effect. Causes of this anomaly hence remain obscure.

The drastic decline in the Bristol Bay red king crab stock was well characterized by survey estimates. It also was predictable on the basis of earlier size-frequency data reflecting the presence of at least one weak year class (Incze et al. 1986). The decline, however, was much faster than forecasted (Fig. 14) and all segments

TABLE 6. Stepwise calculations for predicting abundance[a]

Estimate	Symbol	Calculation	Interpretation
Survey abundance	$N_{i,0}$	$\sum_{K} A_k \overline{D}_{i,k}$	Estimated abundance of the i^{th} size group from a group of strata at the mid-point of the survey period.
a) Available stock	$N_{i,a}$	$N_{i,0}e^{-Ma}$	Abundance at the beginning of the fishing season some (*a*) months after the survey mid-point as determined by the monthly rate of natural mortality (*M*).
b) Escapement	$N_{i,b}$	$N_{i,a}e^{-Z(b-a)}$	Post-season abundance where: $Z = -\ln(1-A)$, $A = m + n - mn$; *m* and *n* are conditional rates of fishing and natural mortality. All rates are applied monthly.
c) Number pre-molt	$N_{i,c}$	$N_{i,b}e^{-M(c-b)}$	Number available at beginning of molting season.
Number molting	$N_{i,l}$	$\frac{1}{2}(N_{i,c} + N_{i,c}e^{-M(d-c)})$	Number of crab at the mid-point (*l*) of a molting period that begins at Time (c) and ends at Time (d).
d) Number post-molt[b]	$N_{i,d}$	$N_{i,l} + \sum_{h} N_{h,l}P_{h,i} - \sum_{h} N_{i,l}P_{i,h}$	Average number molting in i^{th} class plus those growing to the i^{th} group from smaller size groups less those leaving the i^{th} class due to growth. P is a matrix of growth transition probabilities (e.g. P_{ii} is the annual probability of skipping a molt).
e) Predicted survey abundance	$N_{i,e}$	$N_{i,d}e^{-M(e-d)}$	In year following, i.e. e is usually 12.
f) Predicted[c] available stock	$N_{i,f}$	$N_{i,e}e^{-M(f-e)}$	Second season following survey.

[a] These calculations are done in stepwise fashion to allow input of differing seasonal mortality rates to test resultant effects. Calculations can be much simplified if this feature is omitted. Calculations for the present report assume constant mortality in monthly steps.

[b] The growth transition matrix is from Balsiger (1974).

[c] Size specific harvest ratios from the previous season are applied at this point if a 2-yr forecast is desired and steps *b* through *f* are repeated.

of the population declined drastically from 1982 to 1983 (Table 5). Catches account for significant proportions of the legal male stock but fail to explain declines in other segments of the population and subsequent recruitment failure.

Studies of eastern Bering Sea blue king crab stocks have a relatively short history and there is little available information on Asian populations. Until recently these stocks made up small fractions of annual landings (Table 1) and they did not receive priority in resource assessment efforts. Five years ago, it was not predicted that blue king crab would dominate king crab landings in 1983 or that the St. Matthew Island fishery would become the most important. Because so little was known about them, management measures applied to blue king crab stocks were, by default, nearly identical to those for red king crab. Recently, it has become apparent that life histories of the two species differ considerably (Table 4). This situation provides a natural experimental situation for examining the interaction between management measures and biological parameters. Better estimates of the latter are clearly needed for blue king crab stocks.

Blue king crabs are generally associated with rocky areas that are difficult to trawl. They also occupy relatively restricted habitats, and the standard 20 nautical mile grid results in relatively few tows from which to estimate population size. Population estimates for the Pribilof Islands stock (Fig. 15), for example, fluctuated widely prior to 1979 when the sampling grid was augmented by addition of stations at the corners of grid squares. Survey stations were added to the St. Matthew Island area in 1983 after it became apparent that augmented-sampling produced estimates in the Pribilof

TABLE 7. Target exploitation rates (%) for Alaskan king crab stocks (harvest strategy)[a].

		Approximate exploitation rates of legal crab at given levels of postrecruits		
Population size	Prerecruit abundance	Low	Moderate	High
Depressed	Declining	Less than 20	Less than 25	Less than 25
	Stable	30	30	35
	Increasing	30	30	35
Average	Declining	40	40	40
	Stable	40	45	45
	Increasing	40	50	50
Peak	Declining	40	45	50
	Stable	50	55	60
	Increasing	60	60	60

[a] Modified from ADFG (1983). Definitions: (a) population size refers to males and females, (b) prerecruit refers to males that are within one to two molting increments of legal size, (c) postrecruits have been legal for 1 yr (escaped one fishery), and (d) low is less than 1/3 of legal biomass, high is more than 2/3 of legal biomass.

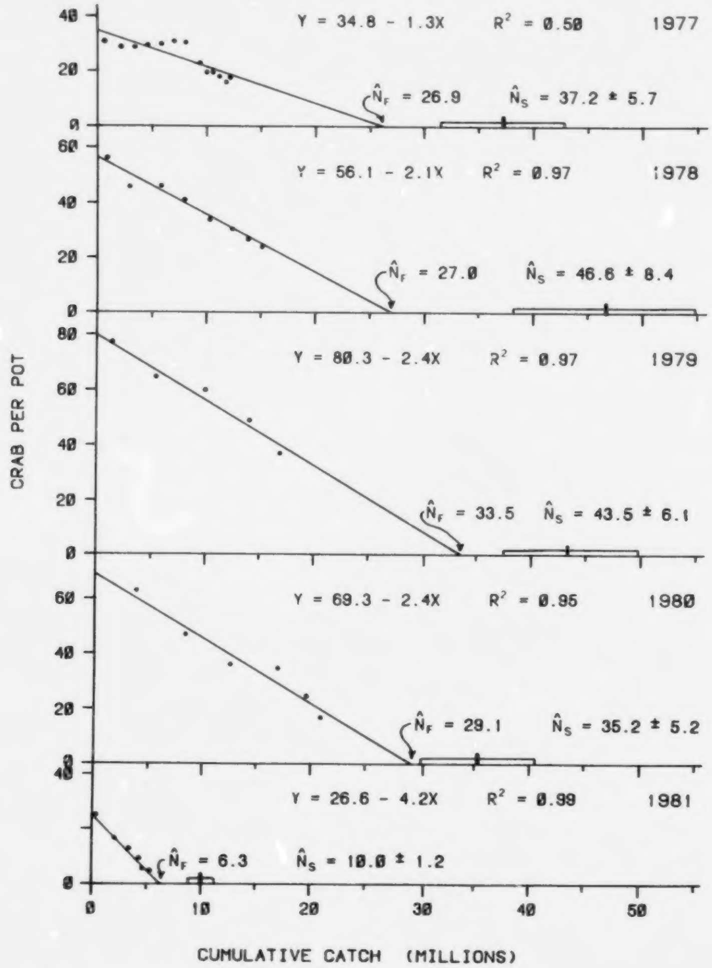

FIG. 16. Comparison of fishery derived Leslie estimates (N_F with survey estimates ($\hat{N}_s$) of legal male abundance for Bristol Bay red king crab. Plotted points represent successive weeks in the fishery. Axes are millions of legal crabs and catch per pot lift.

Islands that were better correlated with commercial fisheries data. Unfortunately, Leslie estimates of legal stock abundance have not been possible either because of low catch rates and lengthy times between landings or, more recently, because seasons have been so short (one month or less) due to the influx of vessels that normally would have fished elsewhere. The validity of survey estimates has hence been difficult to establish.

Adequacy of Management Measures

Alaskan king crab fisheries are regulated by size-sex-season restrictions augmented by target exploitation rates and a variety of other regulations (Tables 2 and 7). During the evolution of regulations, many methods of regulating harvest and gear have been applied. Recent declines in Bering Sea stocks as well as those in other areas of Alaska have led industry to question the adequacy of the management system. The Alaska Board of Fisheries policy of attempting to maintain stability in landings through a series of target exploitation rates has been particularly questioned. Reeves and Marasco (1980) suggest that a simpler size-sex-season approach would lead to the same average yields as the present management strategy. Reeves and Marasco point out, however, that the value of landings may decrease if there is a positive correlation between landed value and the size of crab in the catch.

Limiting regulations to size, sex and season is appealing because of its simplicity. Regulation would be easily enforceable and would not result in season closure when there were marketable crab to be caught. Present size limits, perhaps fortuitously, are approximately at the critical size for maximizing yield per recruit (Balsiger 1974). Mature females without eggs, or with abnormally small numbers of eggs attached to their pleopods during the egg-carrying period, have been observed following large declines in male abundance (Powell et al. 1974). Current size limits seek to prevent this problem by ensuring that males that mature at 100 to 105 mm carapace length (Somerton 1980) may breed at least once (usually twice) before entering the fishery at 135 to 140 mm. Prohibiting the landing of females is also designed to maximize reproductive potential. There has, however, been no demonstration that maximizing egg production produces larger or more stable populations (Incze et al. 1986). The Federal management plan (NPFMC 1984) advocates optimizing the number of mature females. Harvesting females may, hence, be a viable option from a biological standpoint and may actually increase yields. The smaller size of females has, however, virtually precluded interest on the part of the processing industry.

Protection of king crabs during the molting period results in decreased wastage during fishing operations and in higher product quality. Restricting the fishery to pot gear has served similar goals. Season and gear restrictions along with the industry-wide practice of landing live crabs have ensured a product with consistently high quality and value.

Exclusive registration areas and pot limits have served to disperse fishing effort and provide for more easily managed fisheries through indirect effort control. However, they have been controversial because their allocative nature tends to favor local (Alaskan) fishing fleets. Although pot limits have never been applied in the Bering Sea, their use in other areas of Alaska has encouraged operators of larger vessels (predominately non-Alaskan) to fish areas where they could use their mobility and fishing power to maximum advantage. Exclusive registration areas have also had this effect. Limited entry has never been strongly advocated and Bering Sea seasons have been shortened from three months in 1973 to one month in 1982. The record Bristol Bay catch was taken during 6 wk in 1980. Effort control in king crab fisheries has, hence, been indirect and largely ineffective.

The value of effort control in king crab fisheries is difficult to assess, in part, because most king crab vessels are also involved in other fisheries. For example, the same vessels, gear, fishermen, and processing plants that are involved in king crab fisheries also engage in tanner crab fisheries. Both fisheries expanded in the Bering Sea throughout the 1970s (Otto 1981). Capital generated in the king crab fishery financed development of the tanner crab fishery and, it was hoped, would help foster domestic development of ground fish resources. The Magnuson Fishery Conservation and Management Act clearly mandated domestic development leading to the exclusion of foreign fishing in U.S. waters. Japanese tanner crab fishermen were excluded from the Bering Sea in 1980. Political and legal controversy surrounding limited entry in Alaskan salmon and herring fisheries has also, by implication, served as a barrier to consideration of effort control with king crab. From a biological perspective it seems unlikely that further control on fishing effort would have prevented declines in king crab landings. Size, sex, and season regulations had already been in place for over a decade which prevented the fishery from harvesting males before reaching optimum size, and largely precluded the fishery from affecting reproductive potential.

The management system in place has been successful in preventing growth overfishing and in insuring product quality but has clearly not been able to prevent severe declines in abundance, and hence, stabilize landings. The management policy intended to dampen fluctuations in landings is embodied in a variable set of target exploitation rates (Table 7). The intent of variable exploitation rates is to provide for a legal-size stock that is composed of "various age classes" and to "reduce fluctuations associated with annual recruitment" (ADFG 1983). Management recognizes that providing for a carry-over of legal-size crabs may not result in maximizing landings but considers year to year stability in landings as economically desirable. In retrospect, the set of policies and regulations intended to provide more stable king crab fisheries is flawed, principally because there is an implicit assumption that natural mortality rates on prerecruit and legal crab remain fairly constant from year to year. This same assumption is embodied in predictive calculations (Table 6). There are also some problems in interpreting exactly what is meant by terms such as "declining" (no period of time or rate is specified) and when an "average" population becomes a "peak" population. Regardless of interpretation, however, the net result of the current harvest strategy is that exploitation rates considered desirable in a given season are predicated on expectations of recruitment in following seasons.

Recruitment and hence legal stock abundance were predictable over most of the history of the trawl survey (Fig. 14 and 15), however 1-yr forecasts of abundance have been substantially larger than the next year's survey estimates in Bristol Bay since 1980. In discussing causal mechanisms behind the decline of king crab stocks I will focus on Bristol Bay although similar trends have become apparent in blue king crab stocks since 1983. Size-frequency data (Fig. 9–11) and population estimates (Table 5) indicated that abundance of prerecruit males was declining relative to that of legal males in both species. Variable year-class strength was suspected and troughs in size-frequency distributions foreshadowed declining abundance of legal crab.

Observed and predicted abundance of legal crab in Bristol Bay began to show large negative deviations in 1981 (Table 8). Since this occurred following an intensive 1980 fishery with record effort levels, catch and exploitation rates, I considered it possible that handling mortality of sublegal males was reducing recruitment. Calculations (Table 6) following the 1980 fishery gave an estimated recruitment of 10 million crab for 1981 which was large relative to the 1981 survey estimate of 11.3 million legals. Effort remained high in 1981 and, in 1982, projected recruitment was larger than the survey estimate of legal crab abundance. Handling mortality in 1981 would have had to be as large as the 1981 catch to account for the discrepancy (5.6 million) between observed and predicted abundance in 1982 (Table 8). This seemed unreasonable since dead loss in the fishery was negligible. Further, abundance of mature females did not decline much from 1981 to 1982 (Table 5), and it was difficult to explain why handling mortality would not affect females as well as males. Fishing was curtailed by decreased quotas in 1982 and effort declined from 542 000 to 142 000 pot lifts (74%). The disparity between observed and predicted abundance, however, continued to increase in 1983. The degree to which handling mortality affects recruitment still remains unquantified, but is probably small.

Declines in abundance of Bristol Bay red king crab were apparently caused by one or more weak year classes and by a drastic increase in natural mortality. Increased rates of natural mortality were undoubtedly the major cause of recruitment failure (Table 8) and were not predictable through current assessment techniques. Bristol Bay catch never exceeded 60% of the estimated legal stock or 10% of the total population estimate. Since smaller crabs are poorly sampled, total population is under-estimated, and fishing mortality was an even smaller fraction of the population as a whole. Further, declines in abundance of both males and females occurred (Table 5) even though females are not harvested.

Populations of known predators, particularly cod (Wallace et al. 1949), have been at high levels during the 1980s (Sample 1984). During 1981, over 10% of cod stomachs examined contained newly molted red king crab (NMFS unpublished data, A. Shimada, Northwest and Alaska Fisheries Center, pers. comm.). It appears that cod do not prey on king crab except during molting, as studies conducted during other seasons have not found substantial numbers of king crab in cod diets (Feder and Jewett 1981; Jewett 1978). It is, hence, possible that oceanographic conditions that foster co-occurrence of cod and king crab in the same area during the crab molting period could have a substantial effect on mortality rates.

Pathological examination of tissue samples collected in 1981 and 1982 has shown the presence of a previously undescribed microsporidian and one or more viruses (Dr. Albert Sparks, Northwest and Alaska Fisheries Center, pers. comm.). Diseases caused by such organisms have caused epizootics in other invertebrate populations, and such epizootics can be triggered by environmental conditions. Considerable research on causes of natural mortality and their interactions with environmental variables will be necessary to clarify relative contributions of predation and disease.

The development of domestic trawl fisheries for yellowfin sole (*Limanda aspera*) also coincided with

TABLE 8. Predicted abundance, survey estimates, and exploitation rates for Bristol Bay red king crab.[a]

	Predicted		Survey	Deviation		Exploitation	
Year	Recruits	Legals	Legals	Legals	%	Catch	%
1975	12.4	22.7	21.0	−1.7	7.4	8.0	38.1
1976	12.0	21.9	32.7	10.9	49.6	10.4	31.6
1977	20.3	37.3	37.6	0.3	0.9	11.5	30.5
1978	23.8	43.2	46.6	3.4	7.9	14.4	31.0
1979	20.1	43.8	43.9	0.1	0.3	16.6	37.8
1980	17.3	37.0	36.1	−0.9	−2.4	20.5	56.8
1981	10.0	20.9	11.3	−9.6	−45.9	5.2	46.0
1982	6.1	10.3	4.7	−5.6	−54.3	0.5	11.1
1983	6.1	9.3	1.5	−7.8	−83.6	0.0	0.0

[a] Units in millions of crabs, catches differ slightly from Table 3 due to rounding, and predicted values are calculated according to Table 6.

declines in king crab abundance. King crabs are taken as incidental catch in both foreign and domestic trawl fisheries. Incidental catches in 1982 were less than 200 000 crabs in Bristol Bay (Nelson et al. 1984) and it seems unlikely that trawl fisheries account for a measurable fraction of declines in abundance. As a political issue, however, incidental catch of red king crab has been controversial and consequently managers have been under considerable pressure to close all or part of Bristol Bay to bottom trawling.

I conclude that directed or undirected fishing has not been a major cause of population decline in Bristol Bay red king crab. I strongly suspect that fisheries have not been a major cause of population decline in blue king crab because patterns in discrepancies between predicted and subsequent abundance are similar to those for red king crab. Management measures failed to prevent recent declines in landings because causes of declines in abundance are not related to fishing, and hence largely beyond control.

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Sampling of Bivalve Larvae[1]

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Bivalve veliger larvae are small, usually less than 300 μm in maximum dimension, and swim weakly in either vertically oriented straight lines or helices. They have no capability to swim in the horizontal plane; such movement is passive. Active avoidance of net or pumped sampling systems is probably negligible. Representative, quantitative sampling of bivalve veliger larvae throughout the water column is, however, confounded by active depth regulation of larvae in response to pressure, gravity, light, salinity, and temperature stimuli. These responses vary between species and between different developmental stages within a species. Design of sampling protocol requires some prior knowledge of larval swimming behaviour.

Identification of bivalve veliger larvae in formalin preserved samples relies heavily on shape and morphometric measurements. Recently, a combination of optical and scanning electron microscopy techniques have been employed to provide much improved accuracy in identification of bivalve veliger larvae. Identification and enumeration present a limited information set to the fishery biologist. Simple assays of the quality or viability of larvae collected in the field have been lacking; however, recent work with visual lipid specific stains in cultured bivalve larvae has demonstrated a strong qualitative relationship between larval lipid content and ability of those larvae to metamorphose. Lipid is important to bivalve larvae as both an energy reserve and in maintaining low specific gravity. Lipid specific staining can be effected quickly and easily on field collected plankton samples and provides an index of larval condition on individual animals. Present work focusses on development of a quantitative visual assay of larval lipid content which will provide a valuable supplement to data on larval speciation, size, and numbers.

Les larves véligères des bivalves sont petites, ont généralement une taille maximale inférieure à 300 μm, et nagent faiblement dans le plan vertical, en ligne droite ou en spirale. Elles ne peuvent pas nager dans le plan horizontal; ce déplacement est passif. Le nombre d'individus qui évitent les systèmes d'échantillonnage utilisant des filets ou des pompes est probablement négligeable. Cependant, l'échantillonnage représentatif et quantitatif de larves véligères de bivalves dans toute la colonne d'eau est entravé par le déplacement vertical des larves en fonction de la pression, de la gravité, de la lumière, de la salinité et de la température. Ces réactions varient selon l'espèce et les divers stades de développement à l'intérieur d'une même espèce. L'élaboration d'une procédure d'échantillonnage nécessite certaines connaissances préalables du comportement natatoire des larves.

L'identification de spécimens de larves véligères de bivalves conservés dans le formol repose beaucoup sur la forme et les mesures morphométriques. On a utilisé récemment des techniques faisant appel à la microscopie optique et électronique à balayage pour améliorer de beaucoup la précision de l'identification des larves véligères de bivalves. L'identification et le dénombrement fournissent au biologiste des pêches un ensemble limité d'informations. Il n'y a pas eu suffisamment d'analyses simples de la qualité et de la viabilité des larves recueillies sur le terrain; cependant, des travaux récents utilisant des colorants visuels spécifiques aux lipides chez des larves de bivalves d'élevage ont montré qu'il y avait une relation qualitative étroite entre le contenu lipidique des larves et la capacité qu'ont celles-ci de se métamorphoser. Les lipides sont importants pour les larves de bivalves en ce qu'ils servent de réserve d'énergie et permettent de garder un faible poids spécifique. La coloration des lipides peut être réalisée rapidement et facilement sur des échantillons de plancton recueillis sur le terrain, et fournit un indice de l'état des larves chez certains individus. La présente étude est axée sur la mise au point d'une analyse quantitative visuelle du contenu lipidique des larves, laquelle apportera un complément valable aux données sur la différenciation, la taille et la quantité des larves.

Introduction

Bivalve veliger larvae are generally less than 300 μm in maximum dimension, negatively buoyant and swim weakly. Consequently, their ability to actively avoid either towed nets or pumped sampling systems is probably negligible. The major problem encountered in representative quantitative sampling of bivalve veliger larvae in a given water column is, therefore, not one of sampling gear but one of understanding (1) the interaction of physical forces by which bivalve veligers are passively transported and (2) active depth regulation by veligers in response to a number of environmental stimuli. This problem is the focus of the first section of this report. Subsequent sections discuss identification of veligers once they are collected, and methods for estimation of the potential viability or "quality" of larvae.

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Factors Influencing Vertical Distribution and Dispersal of Larvae

Bivalve larvae swim upwards in vertically oriented straight lines while rotating about their dorso-ventral axis or, more commonly, in vertically oriented helices such that one valve is always oriented toward the outside of the swimming path (Bayne 1963, 1964; Cragg 1980; Cragg and Gruffydd 1975; Mann and Wolf 1983). Movement is propelled by the beating of the large, marginal cilia of the velum (Bayne 1976; Cragg 1980). Periods of upward movement are alternated with periods of passive sinking either with the velum extended and beating, thereby retarding the sinking rate (Cragg and Gruffydd 1975; Mann and Wolf 1983) or with the velum retracted (Carriker 1961; Mann and Wolf 1983). Active downward swimming has also been reported (Isham and Tierney 1953; Lough and Gonor 1971). When the veliger adopts a helical swimming pattern the net rate of vertical movement is influenced by the diameter and pitch of the helix in addition to absolute velocity (Cragg 1980; Mann and Wolf 1983). Depth regulation is then effected by alternating periods of upward swimming with passive or actively regulated sinking. Bivalve veligers have no capability to swim in the horizontal plane.

Andrews (1979) reviewed the subject of dispersal of oyster larvae and noted that it was "poorly understood" and that "hydrographic regimes had not been appreciated sufficiently to plan sampling of larvae." Dispersal is influenced by passive and active components; however, the point at which physical forces become sufficient to override any active component has not been adequately examined.

Literature relevant to the distribution and dispersal of bivalve veligers can, for the sake of discussion, be subdivided into three groups. The first of these groups treats bivalve veligers as purely passive particles whose dispersal is at the mercy of physical events. The second group, by far the largest, consists of field observations of horizontal and/or vertical distribution of veligers. Distribution data is usually collected and reported in conjunction with various biological (e.g., chlorophyll and phytoplankton cell concentrations) and physical (temperature, salinity, density) functions, and, from a collective consideration of all data, an inference made of the cause or causes of observed distribution. The third group consists of behavioural data obtained from laboratory experiments in which usually one of an array of stimuli (e.g., temperature, light, salinity, pressure) is systematically varied while the others are maintained at constant level. These data are reported as either absolute rate measurements of swimming velocity in relation to set conditions, threshold levels of a specific stimulus required to elicit quantitatively discernable changes in swimming behaviour, or both. In turn the behavioural data can be (1) superimposed directly on physical data collected from the field to provide a purely descriptive and predictive model of larval occurrence, (2) examined in conjunction with field distribution data to provide further substantiation of the inferred causal relationships, or, (3) in the form of a numerical predictive model, compared directly with descriptive distribution field data as a "double black box" approach to emphasize areas of close agreement and greatest discrepancy. The latter approach is particularly useful in delineating research subject areas that are worthy of further experimental investigation.

Boicourt (1982) describes how purely physical processes can explain observational differences in the occurrence and concentration of veliger larvae of the oyster *Crassostrea virginica* (Gmelin) in two adjacent tributaries of the lower Choptank River (Chesapeake Bay). One of these tributaries, Broad Creek, has, over the past 40 years, exhibited consistently greater oyster spatfall than the adjacent tributary, the Tred Avon River. The geometry, fresh water flux, temperature, salinity and biology of the tributaries are similar; however, current meter and dye dispersion programs illustrate that larval recruitment to the Tred Avon is restricted to larvae originating in the Tred Avon itself whereas exchange processes between Broad Creek and the Choptank River allow the former to supplement its larval settlement with larvae from the latter. Boicourt (1982) further emphasizes two factors relevant to the subject of sampling bivalve veligers. The first is that horizontal currents clearly dominate larval transport because daily transport distances of the order of kilometers per day are commonplace in coastal or estuarine systems. The second is a problem of scale: traditionally physical oceanographers have worked on mesoscale problems. While this concentration of effort may be meaningful to the zoogeography of major oceanic basins it has contributed only marginally to coastal and estuarine problems where a "meaningful biological scale" may be of the order of meters in the vertical scale and tens to hundreds of meters in the horizontal. Clearly, increased focus on smaller scale coastal or estuarine problems by physical oceanographers would enhance our understanding of the biology of these regions. This is especially so with bivalves in that with relatively few exceptions (e.g., Tarnowski 1982; Mann 1985) intensive field studies of bivalve larvae have been restricted to estuaries.

Working on the same estuaries as Boicourt (1982), Seliger and co-workers (1982) effected nearly synoptic measurements of physical hydrographic parameters and sampling for oyster veliger larvae along axial transects of both estuaries. The observations of Seliger et al. (1982) support Boicourt's conclusions in that *C. virginica* larvae originating in surface waters of Chesapeake Bay may on a flood tide be carried (presumably passively; this is not directly discussed) below the lower salinity surface waters of the Choptank River and, eventually, into its Broad Creek tributary. Seliger et al. (1982) conclude that "Where stratification is persistent the water density isopleth distributions and vertical stabilities could be used to infer the potential for upstream transport and retention."

Andrews (1979) illustrates, through a listing of previous works, the wide variety in the morphometry, tidal range and fresh water input of coastal sites where intensive field studies of bivalve veliger occurrence and dispersal have been made. The works of Carriker (1961), Medcof (1955), Quayle (1964, 1969), and Korringa (1941) all illustrate low loss of larvae per tidal cycle in a variety of systems which exhibit low freshwater input but a variety of tidal ranges. These works suggest that physical dilution is the major influence on the number of larvae retained or lost in the systems examined and that, in these instances, larval behaviour is of relatively little importance.

The role of behaviour in estuarine retention of larvae has been the subject of intense discussions for over 70 years. The stimulus for these discussions began with the works of Julius Nelson and his son Thurlow C. Nelson in Little Egg Harbor and Barnegat Bay, N.J. and Delaware Bay (Nelson 1911; Nelson 1953, 1955). They examined the distribution of oyster veliger larvae at these sites in relation to the position of the parental broodstocks. Where tidal currents were small the larvae were found on both the ebb and flood tide in equal numbers whereas in stronger tidal regimes larvae predominated on the flood tide. Older larvae were progressively more abundant upstream than younger larvae. Also, older larvae tended to be more abundant deeper in the water column. In 1911 Julius Nelson proposed that oyster veliger larvae, especially older larvae, effect retention or upstream movement in estuaries by depth regulation to take advantage of alternating tidal currents. The proposed stimuli for these vertical excursions were tidally associated salinity and current velocity changes. Field work subsequent to that of the Nelsons by Carriker (1951) in New Jersey estuaries and Kunkle (1957) in Delaware Bay further described a greater abundance of larvae on the flood than ebb tides and a preponderance of older veligers near the bottom.

Experimental work to supplement the field observations was also forthcoming. T. C. Nelson and E. B. Perkins (1931) reported that "eyed" larvae of *C. virginica* maintained in glass dishes were stimulated to swim by the introduction of higher salinity water and, conversely, inactivated by lower salinity water. Haskin (1964) demonstrated increased activity of *C. virginica* veliger larvae when salinity increased from 7 to 14 ppt. Hidu and Haskin (1978) expanded this approach and measured swimming velocities of *C. virginica* larvae at a variety of salinities and temperatures. They suggested that veligers of increased size could swim faster, and that this ability may contribute to better depth regulation and partially explain the field observations of Carriker (1951) and Kunkle (1957). As will be discussed later in this paper, such ontogenetic changes in swimming ability are not always evident in other bivalve veligers.

The Julius Nelson hypothesis of net transport of veliger larvae in an upstream direction in estuaries received further attention from Pritchard (1951, 1952). Pritchard proposed a two layer counterflow estuarine system in which fresher surface water flowed seaward while higher salinity water penetrated upstream along the bottom. The junction of the two layers represents a region of no net flow. He suggested that the deeper, more saline water carried veliger larvae upstream in the James River, Virginia. The eventual upwelling of this water on the northeast side of the river is suggested by Andrews (1979) to be the probable source of consistent oyster spatfall in that region. In a later study of the same river Wood and Hargis (1971) compared the distribution of *C. virginica* veliger larvae to that of coal particles of a similar size and density. Differences were evident in that the greatest concentration of coal particles, here acting as passive drifters, coincided with the region of highest current velocities whereas veligers appeared to rise and sink with salinity changes associated with flood and ebb tide.

Observational field evidence for upstream or no net movement of planktonic larvae through depth regulation in layered (with respect to salinity) estuarine systems is not restricted to bivalve larvae. Similar comments have also been made with respect to the larvae of barnacles (Bousfield 1955)[2] fish (Fortier and Leggett 1983), brachyuran crabs (see contributions in Kennedy, 1982; review by Sulkin 1984 and literature therein) and even dinoflagellates (Tyler and Seliger 1978, 1981). Despite this weight of opinion the original J. Nelson hypothesis is still subject to considerable criticism. Andrews (1979) presents and discusses a series of data collected at the same time and locale as that reported by Wood and Hargis (1971). Andrews data "reveal regular rhythms of larval abundance with tidal stage," and he concluded that "larvae were being recruited continuously by newly spawned broods," that "no vertical stratification of larvae occurred, except that fewer larvae were found in surface and bottom samples" and that "the distribution of bivalve larvae in the James River is passive and dependent upon tidal currents and mixing." Spat settlement data from a grid of 19 stations of cultch collectors showed synchronous increases and decreases in larval settlement on a river wide basis suggesting that larvae occur in swarms that become dispersed throughout the river prior to settlement. Andrews (1979) also critiques the data of Haskin (1964) concerning larval occurrence in the Delaware Bay. Haskin explains tidal variations in larval concentration by inferring cyclical rising and sinking of the larvae; however, Andrews (1979) suggests that the same observations could result from sampling the upstream sector of a larval swarm carried en mass by tidal excursions without the need for inference of vertical migration.

Korringa (1941), examining the distribution of *Ostrea edulis* L. larvae in the Oosterschelde (Netherlands), found that his data could not be explained by J. Nelson's hypothesis. Korringa (1952) was equally critical of Carriker's (1951) data on *C. virginica* and remained unconvinced that tidally synchronized vertical migrations were important in the upstream movement of bivalve larvae in estuaries. Thus, despite the relative abundance of literature on observational studies of the distribution of bivalve larvae in a number of different estuaries of differing character there is no consensus of opinion on any one mechanism to explain retention or net upstream movement of larvae within an estuary or spatial variability patterns in settlement of juvenile stages. This variety of opinion may in fact reflect a true variety in predominant mechanisms for larval retention with both active and passive processes contributing to the observed distributions.

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[2] In contrast, deWolf (1973, 1974) concludes that barnacle larvae can be retained in estuaries by purely passive means.

Design of sampling regimes on continental shelves is generally less complicated than estuarine systems in terms of tidally related current counterflow regimes and salinity stratification. Work in these regions has, however, been far less intense, probably due to the comparative lack of both economic interest in shelf dwelling bivalves and of adequate keys for identification of their veligers. Tarnowski (1982) sampled surf clam (*Spisula solidissima* Dillwyn) larvae along two transects off southern New Jersey from spring 1976 to fall 1978. Peak larval concentrations were related to spawning periodicities of adult clams residing above and below the seasonal thermocline. No details are given of sampling method used, depths of sample collection, or the relationship of larval distribution to hydrographic factors. Mann (1985) examined seasonal changes in depth distribution of bivalve larvae from April to December 1981 at a station on the Southern New England Shelf. Depth stratified samples were taken at intervals of 10 m using a Clarke–Bumpus net. Larval distribution was observed to be limited to depths below the intense seasonal thermocline during the summer months; however, following the degradation of the thermocline in the fall months larvae were found throughout the water column. The seasonal intense thermocline is a conservative feature of the Southern New England Shelf and Middle Atlantic Bight (Bigelow 1933; Ketchum and Corwin 1964; Beardsley et al. 1976; Beardsley and Boicourt 1980) and the aggregations by depth of larvae observed by Mann are probably representative of this large zoogeographical region. Attempts to estimate horizontal dispersal, a function of depth specific current velocities, were not made by Mann. Indeed, the review of Beardsley and Boicourt (1980) of data available to that date illustrate both the lack of suitable depth specific data for this exercise and further reiterate Boicourt's (1982) comments on the inequity of relevant scales as viewed by biologists and physical oceanographers. The meaningful biological scale in depth measurement in the system examined by Mann is of the order of meters; discrete, long-term current velocity measurements have not been made on this scale. Mann's observations do, however, provide an interesting comparison to those made in estuarine systems in that they suggest that active depth regulation by the veliger larvae in response to an overlaying thermal "barrier" determines depth distribution during the summer period whereas wind driven mixing of the water column in the fall and winter months determines depth distributions at that time. The summer–fall transition represents one in which active depth regulation is supplanted by passive distribution at the mercy of physical mixing. Clearly both active and passive processes may be important and effective on the continental shelf in just the same way as both may be effective in estuarine systems.

Swimming behaviour and depth regulation in bivalve veliger larvae has been examined in laboratory systems by a number of authors. The stimuli of gravity, pressure and light present predictable, conservative gradients to which motile larvae can orient. Changes in temperature and salinity are, however, not conservative with respect to gradient or orientation. It is important to note that in any water column the stimuli of gravity and pressure are always constant, thus any experimental protocols examining changes in light, temperature or salinity are in fact examining reinforcement of or opposition to geotactic and barotactic responses. A comprehensive discussion of appropriate terminology is given by Sulkin (1984).

In static laboratory containers healthy trochophore and veliger larvae swim continuously (Andrews 1979; Cragg 1980; Mann and Wolf 1983; and personal observations). *Mytilus edulis* L. trochophores show no oriented response to light or gravity (Bayne 1964) whereas those of *Pecten maximus* L. (Cragg 1980) and *Arctica islandica* (Mann and Wolf 1983) are negatively geotactic. The trochophores of *A. islandica* show no phototactic or barotactic response. Veliger larvae are generally negatively geotactic but exhibit variable phototaxis (Bayne 1964; Andrews 1979; Cragg 1980; Mann and Wolf 1983). The "surface seeking" behaviour of both *M. edulis* and *P. maximus* changes as the pediveliger stage of development is attained; a photonegative, geopositive behaviour becomes prevalent (Bayne 1964; Cragg 1980).

Veliger larvae of several species of bivalves have been examined for their response to changes in pressure. Bayne (1963) reports that, at atmospheric pressure, veliger larvae of *M. edulis* swim slowly in broad helices; however, on increasing pressure the vertical component of the helix increased and the horizontal component decreased resulting in increased mean vertical velocity. The threshold increase in pressure required to elicit this response was <0.54 bars. The eyed veliger stage of *M. edulis* exhibited a positive but somewhat smaller response to increased pressure whereas the pediveliger larvae exhibited no response. The combination of data for *M. edulis* larvae (Bayne 1963, 1964, 1976) suggest that veligers remain at the surface while pediveligers move towards the bottom. Cragg and Gruffydd (1975) examined swimming response to changes in pressure of veligers of *Ostrea edulis*. The threshold pressure change required to elicit response increased from <0.1 bars in young veligers to between 0.1 and 0.2 bars at 11 d after release. This compares with a threshold of <0.1 bars for *Mercenaria mercenaria* L. larvae (Haskin 1964). As with young *M. edulis* veligers, *O. edulis* veligers increased mean vertical velocity under increased pressure through rate adjustments of the components of the helical swimming path (Cragg and Gruffydd 1975). Veliger larvae of *P. maximus* and *A. islandica* also swim upwards in response to increased pressure (Cragg 1980; Mann and Wolf 1983). The threshold pressure to elicit response in *A. islandica* veligers (<0.5 bars) is, however, considerably lower than that for *P. maximus* (1.0–1.2 bars depending upon age).

Direct examinations of the influence of temperature gradients on the swimming of bivalve veligers are limited to those reported by Mann and Wolf (1983) for *A. islandica*. Indirect examination of both temperature and salinity optima have, however, been made in several studies designed to identify optimal condition for large scale culture of larvae of selected bivalve species (Walne 1965, 1966; Helm and Millican 1977).

Laboratory data on the growth and behaviour of veligers in relation to changes in environmental parameters can be of use in interpreting or predicting larval occurrence in systems where active depth regulation is not negated by physical forces. Such laboratory data does, at present, have limitations in that experiments to examine the influence of changes of more than one stimulus at any one time have not been adequately addressed. Consequently the hierarchial order of the stimuli in eliciting changes in behaviour has not been determined. Note that such a task involves the examination of stimuli thresholds throughout larval development for these are liable to change.

Depth regulation can only be effective in influencing horizontal dispersal processes if the mean rate of vertical movement is sufficient to maintain larvae in the appropriate strata. Mileikovsky (1973) reviewed the speed of active vertical (upward) movement of pelagic larvae of marine benthic invertebrates; most fall in the range 0.67 to 2.00 $\mathrm{mm \cdot s^{-1}}$. Mann and Wolf (1983) reviewed data for bivalve larvae. Published values include 1.17 to 1.33 $\mathrm{mm \cdot s^{-1}}$ for *M. mercenaria* (Turner and George 1955), 7.7 $\mathrm{mm \cdot s^{-1}}$ for *Teredo bartschi*[1] (Isham and Tierney 1953), 1.1 to 4.0 $\mathrm{mm \cdot s^{-1}}$ for *M. edulis* (Konstantinova 1966; Bayne 1976), 0.75 to 10 $\mathrm{mm \cdot s^{-1}}$ for *C. virginica* (Wood and Hargis 1971; Hidu and Haskin 1978), 1.23 $\mathrm{mm \cdot s^{-1}}$ for *O. edulis* (Cragg and Gruffydd 1975), 0.17 to 0.46 $\mathrm{mm \cdot s^{-1}}$ for *P. maximus* (Cragg 1980) and 0.2–0.52 $\mathrm{mm \cdot s^{-1}}$ for *A. islandica* (Mann and Wolf 1983) (surprisingly values for sinking rate are less well documented). In only one of these reports, that of Hidu and Haskin (1978) on *C. virginica*, did mean velocity appear to increase regularly with increasing larval size. The data for *P. maximus* and *A. islandica* are generally lower than for other species; however, this may reflect the experimental temperatures (14 and 13°C, respectively) employed in the cited reports and the colder water habitats of both species. With these two exceptions the values for mean vertical velocity of swimming in bivalve veligers are generally comparable to or higher than the values reported by Mileikovsky (1973). A vertical velocity of 1 $\mathrm{mm \cdot s^{-1}}$ allows movement of 3.6 $\mathrm{m \cdot h^{-1}}$. As most of the swimming rates for bivalves in estuarine systems exceed 1 $\mathrm{mm \cdot s^{-1}}$ it is probable that depth regulation can indeed be effected over biologically meaningful depths in reasonable periods of time. In estuarine systems with pronounced depth stratified counterflow current systems, selection pressure appears to favour species whose larvae exhibit sensitive depth regulatory capabilities, that is those with low threshold stimuli to pressure and higher mean vertical swimming velocities. By contrast those species generally restricted to the shallow continental shelf (e.g., *P. maximus, A. islandica*), where intense vertical stratification is usually less pronounced than in estuaries, have a lesser requirement for such depth regulatory and swimming abilities.

To date attempts to synthesize data from laboratory culture and behaviour experiments with physical data from the field to develop numerical predictive models of larval occurrence have been rare. Boicourt (1982) and Kelley et al. (1982) have discussed this option for brachyuran crabs but only Mann (1986) has both effected the modelling exercise and compared the resultant model to field observations of larval distribution for bivalves. The formulation and testing of such models for estuarine bivalve species would be an admirable research objective for future attention for it is only through such syntheses that we can begin to truly utilize the data available to date, highlight deficiencies for future attention and eventually understand the interaction of biological and physical forces that determine larval distribution. Armed with this knowledge we can then design sampling protocols which will indeed give realistic representations of larval distribution in the field. Until this knowledge is available the design of sampling regimes can follow one of two options. The first is the use of depth integrated sampling by oblique net tows. While this will capture representatives from all depths it provides no data on depth distribution, a particular problem in stratified systems where information on horizontal dispersal is required. Alternatively depth stratified tows may not give representative sampling of the species present and be influenced by any tidally or diurnally stimulated changes in depth regulation.

Identification of Bivalve Larvae

Rees (1950) discusses identification of bivalve larvae based on shell shape, texture, and larval hinge morphology; however, the majority of keys for the identification to genus or species level of bivalve veligers obtained from field plankton tows have relied predominantly upon gross morphometric measurements (see for examples Chanley and Andrews 1971). The characteristics generally used include shell length, height and depth, and the length of the "straight hinge line" (Loosanoff et al. 1966; Chanley and Andrews 1971; Chanley and Chanley 1980; Chanley and Dinamani 1980). Discrimination using differences in shape are dependent upon consistent orientation of specimens. Colour and texture of larvae are markedly influenced by fixation technique, length of time for which the specimen has been archived and the original physiological status of the specimen. Some species exhibit a larval byssal notch, some have an eyespot during the latter stages of larval development, and others have apical cilia (Chanley and Andrews 1971; Culliney and Turner 1976; Turner and Boyle 1975). While keys based on shell shape have proven adequate for use in regions where a limited number of species are represented and where those species are themselves characterized in the later stages of larval development by unusual morphometry

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[1] Although described as *Teredo* (*Lyrodus*) *pedicellata* de Quatrefages by Isham and Tierney (1953) this species was later shown to be *Teredo bartschi* Clapp by Turner and Johnson (1971).

(e.g., the skewed umbonal protruberance in the genus *Crassostrea* or the marked assymetry of the *M. edulis*) they have proven inadequate in the unambiguous identification of larvae of many bivalve species, especially so with early (straight-hinge) veligers. Recently the scanning electron microscope has been used to develop Rees' (1950) approach and provide exacting means for examining the hinge (provinculum) structures of the early life history stages (both veliger and post settlement) of various bivalve molluscs (Calloway and Turner 1978). Such structures may be diagnostic at the generic or specific level (Calloway and Turner 1978; Lutz et al. 1982a, b and extensive literature quoted therein). Using scanning electron microscopy with strictly controlled orientation of the valves Lutz et al. (1982a) illustrate marked differences in the hinge structures of the larvae of a number of bivalve species in addition to subtle changes of shell shape. Lutz et al. (1982b) illustrate a comprehensive format for the presentation of early life history data for bivalve species which includes detailed information on morphometric change during growth and development, photomicrographs of developing larvae, and scanning electron micrographs of whole, disarticulated valves and the characteristic hinge region. Obviously, it is not feasible to examine all plankton tows with the scanning electron microscope. The features of the hinge region described by Lutz et al. (1982a, b) are, however, clearly seen using a compound microscope in conjunction with a strong incident light source. A high intensity fibre optic light source is ideal for this purpose in that oblique lighting may be used to increase contrast in the specimen. Alternatively a number of incident light optical systems, originally designed for epifluorescent microscopy or industrial application in examination of computer circuitry, can be easily modified for routine use in this application. Depending upon the size and morphology of the specimen, and magnification and depth of field of the particular optical system in use observation of all of the hinge features may require the operator to focus in several different planes. For original descriptions, however, the scanning electron microscope is needed to illustrate the three dimensional structure of the hinge region.

The use of both gross morphometric measurements and the more subtle changes in hinge morphology can provide a means for practical identification of most bivalve veligers. A continuing effort to produce a comprehensive key of bivalve early life history stages, through description by light and scanning electron microscopy of cultured specimens as suggested by Lutz et al. (1982a, b), is necessary if field studies of bivalve larvae are to be successful, especially on the continental shelves where the larvae of endemic species are still inadequately described. An integral part of the development of a comprehensive larval key is the maintenance of voucher specimens in laboratory collections and, if possible, in museum collections. The value of voucher specimens to work with adult marine molluscs has long been recognized; however, corresponding specimens of the larval and juvenile stages of most marine molluscs are usually very poorly represented in museum collections.

Assessment of Larval Viability

In contrast to the reasonably extensive literature on the identification of pelagic marine larvae comparatively little attention has been given to development of a simple, practical means of assessing viability of larvae collected in plankton hauls. While certain physiological (e.g., oxygen consumption by microrespirometer, Mann and Gallager 1984) or biochemical (e.g., DNA/RNA ratios, Bulow 1970; Buckley 1979, 1980) indices of physiological condition are available for marine larvae they are impractical for field use in that they require expensive or delicate apparatus, highly skilled operators, considerable time to effect analysis, and above all usually cannot be applied to individual organisms. An alternative to the above physiological and biochemical approaches is available: that of direct examination of nutritional status of individual organisms by histochemical stains.

Lipid has been shown to be a major energy reserve in the planktonic larvae of fish (Ehrlich 1974; Ehrlich and Blaxter 1974; Cetta and Capuzzo 1982) barnacles (Holland and Walker 1975; Lucas et al. 1979; Costlow 1982) and bivalves (Holland and Spencer 1973; Holland 1978; Gallager and Mann 1981; Mann and Gallager 1984, 1985; and unpublished data). The non-feeding cyprid larvae of the barnacle *Balanus balanoides* L. contains numerous oil droplets which are gradually consumed during a period of searching for a suitable settlement substrate. If a substrate is not located by the time approximately 50% of this lipid reserve is utilized insufficient remains for the cyprid to complete metamorphosis to the juvenile stage and death results (Holland and Walker 1975). There would, then, appear to be a threshold lipid requirement for cyprid larvae initiating metamorphosis if completion is to be attained (Crisp 1984). Recently Gallager and Mann (unpublished data) effected a series of experiments during which the newly released veliger larvae of *O. edulis* L. of differing lipid contents (mean values of 14, 11, and 7% of ash free dry weight) were cultured in identical conditions. All exhibited similar growth rates yet the percentage of the larvae present completing metamorphosis (88, 11, and 0%, respectively) differed markedly and suggested a threshold lipid requirement similar to that described by Holland and Walker (1975). Further experiments on *M. mercenaria* by Gallager and Mann (1985a) were designed to examine the rate of growth of straight hinge stage veligers with high and low lipid content respectively cultured under identical conditions. The relationship of resultant pediveliger lipid content to the ability to complete metamorphosis reiterated the above results and further support the suggestion of a lipid threshold requirement. It does not therefore seem unreasonable to suggest that a simple, visual index of lipid content would be a reasonable indicator of larval viability.

Use of lipid content as an index of nutritional status has been suggested previously by Costlow (1982) for *Balanus eburneus* and Tessier and Goulden (1982) for three species of the freshwater cladoceran *Daphnia*. Costlow (1982) suggests that total lipid reserves in *B. eburneus* nauplii can be estimated from the total volume of the "oil cells" which are attached to the outer surface of the midgut. Unpublished data from plankton tows taken by the author near Woods Hole, Massachusetts, illustrate that in locally occurring barnacle nauplii and cyprids not all of these "oil cells" give a positive staining reaction with the lipid specific stain Oil Red O (C.I. 26125). It is not uncommon to find in stained individuals a brightly stained "oil cell" directly abutting a perfectly clear "oil cell." The approach of Costlow (1982) should therefore be used in conjunction with an appropriate staining procedure; even then the suggested direct measurement of the dimensions of each "cell" and subsequent summing makes the method extremely tedious to use on large numbers of individuals. Tessier and Goulden (1982) rely upon the natural carotenoid based pigmentation for ease of identification of the lipid droplets in *Daphnia* species. Based on number and size of droplets they index animals on a subjective rank-score system. Their approach is semiquantitative and has several inherent problems. These include "Scorer bias," the "index is inappropriate for detecting subtle differences and should only be used when large differences exist" and "even though storage at 4°C slows down the color fading (due to caroteroid oxidation) it is difficult to score animals that have been preserved >48 hrs."

Although valuable, neither the approach of Costlow (1982) or Tessier and Goulden (1982) offers both the convenience of use and the truly quantitative capabilities of the method proposed here: namely the use of lipid specific staining in conjunction with either scanning densitometry, photometry or microspectrofluorometry. A number of lipid specific stains are commercially available. Ideally a viability assessment method should use a dye specific for neutral triglycerides in that these are the major energy substrates in bivalve larvae (Holland 1978). Oil Red O, the dye used by Gallager and Mann (1981), stains both triglycerides and phospholipids, the latter being predominantly structural. Oil Red O will detect changes in triglyceride content, but as a component of total lipid content change. Although this appears less than ideal extensive practical experience with this stain has illustrated both its extreme sensitivity and long term stability when used in the staining of cultured bivalve larvae (see Gallager and Mann 1981, 1985b). Changes on the order of nanograms of lipid per individual larvae are readily discernable, the technique is simple and quick, and stained larvae can be archived for extensive periods of time (indeed it is the long term stability of Oil Red O stained specimens which makes it a preferred stain for use in standard teaching preparations in medical and veterinary schools).

Three optical methods exist for obtaining quantitative values of lipid content from stained specimens. These are scanning densitometry, photometry and microspectrofluorometry. The first two use visual stains, the latter a fluorescent stain. All are well-established tools for use in research yet only photometry has been used for the examination of marine larvae as proposed here. Traditionally these techniques have been used on uniform sections of ten microns or less thickness. Calibration for such application is relatively straight forward (Mendelsohn 1966). Whole bivalve larvae often exceed two hundred microns in thickness and are neither flat nor uniform. Calibration is, however, a tractable proposition. Gallager and Mann (1985b) present a modification of Mendelsohn's technique which corrects for absorption by the larval shell and a description of calibration of photometric readings against analytically derived values for larval lipid content. Careful examination of each stain is required because each lipid class may exhibit different staining intensity per unit weight with each stain. Such problems are however, easily overcome by readily available methods and, in the viewpoint of the author, represent necessary groundwork in technique development rather than unsurmountable complications.

Clearly, the lipid staining technique has value in the laboratory and commercial hatcheries as a tool to assay larval condition and predict ability to metamorphose (Gallager and Mann 1985a). The question remains as to whether the technique can be practically used in the field. Ideally this would require a sequential protocol whereby plankton are retained in a net, relaxed, fixed, stained with a suitable visual or fluorescent dye, and examined shipboard for lipid content in addition to the usual morphometric data. In extreme circumstances the author has simplified this approach considerably: plankton were fixed and stained simultaneously by concentration on an appropriate sized mesh, blotting dry and direct immersion in Oil Red O dissolved in ethylene glycol as prepared by Gallager and Mann (1981). General application of this simplified approach is easy to effect and would add a new dimension, that of estimation of larval viability at the individual level, to the data traditionally collected by plankton biologists without detracting from the ability to simultaneously collect the latter data or archive specimens. The development of lipid specific staining techniques for rapid assessment of larval viability at the individual level in the field continues to be a major focus of research in the authors laboratory.

The importance of lipid in the energy metabolism of bivalve larvae has further ramifications on the subject of depth regulation and dispersal. Bivalve larvae have essentially no capacity for anaerobiosis (see discussion in Mann and Gallager 1985). The velum is used for swimming, feeding, respiration, and uptake of dissolved amino acids (Manahan and Crisp 1983). Any cessation or reduction in swimming results not only in sinking but also a marked decrease in rate or cessation of other functions. A reduction in feeding causes depletion of lipid reserves (Holland and Spencer 1973; Gallager and Mann 1981), an increase in specific gravity and an increased problem in swimming. It is therefore not unreasonable to suggest that a marked reduction in swimming activity can only be tolerated for short periods for both respiratory and specific gravity reasons. Indeed Thorson (1950) comments that larvae resembling specimens starved in the laboratory are rarely found in the plankton — this may be because any such "low quality" larvae had already depleted their reserves to the point where they became very dense, sank, and were subsequently eaten by a benthic filter feeder or deposit feeder. Thus, while larvae may depth regulate over tidal cycles as suggested by the J. Nelson hypothesis it is highly unlikely that they at any time settle to the bottom prior to their achieving competency to metamorphose.

Conclusions and Recommendations

Despite extensive work in both the field and laboratory the mechanisms influencing bivalve larval distribution are still poorly understood. Both active processes, in the form of depth regulation by larvae in response to a variety of stimuli, and passive movement at the mercy of physical events appear to contribute to larval dispersal although the point at which physical processes become sufficiently vigorous to negate biological processes has not been addressed. Generalizations concerning active regulation cannot be made in that gradients of non-conservative stimuli to swimming (e.g., temperature and salinity) differ between estuarine and continental shelf environments as do the threshold responses of endemic species to these stimuli.

Representative, quantitative sampling of bivalve larvae in any water column requires some prior knowledge of both physical stratification (including cyclical variation in that stratification in tidally influenced systems) and the behaviour of the larvae per se. Rarely do such data bases exist. Comprehensive physical data acquisition should, whenever possible, accompany sampling of biological entities. In the absense of adequate data bases a combination of depth integrated and depth stratified sampling techniques should be used.

Attempts to synthesize, from laboratory and field data, comprehensive numerical models of larval occurrence and behaviour should be encouraged for it is through this process that subject areas in need of future attention can be most easily defined.

Extreme care is needed in larval identification, especially in coastal or continental shelf regions where the descriptions of the larval forms of endemic species are inadequate. Workers are encouraged to use both gross morphometry and hinge morphology in identifying larvae. A need for a comprehensive key that adequately describes ontogenetic changes in terms of photomicrographs of live specimens and scanning electron micrographs of the external and internal surfaces, and hinge regions of the disarticulated valves is evident.

Simple, optical techniques for real time assessment of viability of individual larvae are available. They offer, for the first time, the ability to measure physiologically meaningful data in addition to the traditionally collected information on size, abundance and speciation.

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A Conceptual Model for Recruitment of the Blue Crab, *Callinectes sapidus* Rathbun, to Estuaries of the Middle Atlantic Bight[1]

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SULKIN, S. D., AND C. E. EPIFANIO. A conceptual model for recruitment of the blue crab, *Callinectes sapidus* Rathbun, to estuaries of the Middle Atlantic Bight, p. 117-123. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

The portunid crab *Callinectes sapidus* spawns near the mouth of the estuary. Both tidal and residual circulation contribute to rapid export of larvae from estuaries of the Middle Atlantic Bight to the continental shelf. Recruitment of the year-class back to the estuary occurs at the megalopa or early juvenile stage. Recruitment success depends primarily on two processes: retention of larvae within the Middle Atlantic Bight and transport of megalopae and juveniles back to the estuary. The former process depends upon seasonal wind-driven reversal of near-shore currents so that entrainment and loss of larvae in the Gulf Stream is prevented. The mechanism for onshore transport remains to be described definitively. Available evidence is consistent with the hypothesis that as megalopae approach metamorphosis, they move from the surface to deep water that exhibits shoreward residual drift on the shelf. Onshore transport in this fashion may be augmented by selective activity on flood tides as megalopae approach the estuary.

Evidence suggests that physical factors regulating larval dispersal are paramount in establishing year-class strength. Although predictive models that can relate climatic events on the shelf to the dispersal process may be developed eventually, forecasts presently must be based on abundance estimates of juveniles after they have migrated into the estuary. Spatial and temporal vagaries in abundance must be interpreted on the basis of climatic events which govern larval dispersal.

Le crabe portunidé *Callinectes sapidus* fraie près des embouchures des estuaires. La circulation due aux marées et la circulation résiduelle favorisent le déplacement rapide des larves des estuaires de la zone du Middle Atlantic Bight vers le plateau continental. Le retour de la classe annuelle dans les estuaires se produit au stade de mégalopes ou au début de celui de juvéniles. Le succès de ce recrutement dépend surtout de deux processus : la rétention des larves dans le Bight et le transport des mégalopes et des juvéniles vers les estuaires. Le premier est fonction du renversement éolien saisonnier des courants de rivage qui permet d'éviter que des larves ne soient entraînées et perdues dans le Gulf Stream. Le mécanisme du transport vers la côte n'a pas encore été décrit de façon précise. Les données disponibles sont cohérentes avec l'hypothèse voulant que les mégalopes, lorsqu'elles approchent du moment de la métamorphose, se déplacent de la surface vers les eaux profondes du plateau subissant une dérive résiduelle en direction de la côte. Ce transport vers la côte peut être favorisé par une utilisation sélective du courant de flot quand les mégalopes s'approchent des estuaires.

Les données indiquent que les facteurs physiques régissant la dispersion des larves jouent un rôle prépondérant dans la détermination de l'importance de la classe d'âge. Il sera sans doute possible d'élaborer des modèles de prévision établissant des relations entre les conditions climatiques du plateau et le processus de dispersion mais, actuellement, les prévisions doivent être basées sur les estimations d'abondance des juvéniles après leur migration dans les estuaires. Les écarts imprévisibles des paramètres spatiaux et temporels de l'abondance doivent être interprétés en fonction des conditions climatiques régissant la dispersion des larves.

To develop effective techniques to forecast year-class strength and to interpret spatial and temporal vagaries of abundance of blue crab stocks, it is necessary to understand the mechanisms that regulate the recruitment process in nature. Presented here is a conceptual model for regulation of recruitment of the blue crab, *Callinectes sapidus*, to estuaries of the Middle Atlantic Bight region of the east coast of North America. The model is based upon extensive field sampling of larvae, experimental work on larval behavior, and characterization of the hydrodynamics of the region.

Although *Callinectes* is primarily a tropical, marine genus, *C. sapidus* has spread to the temperate zone and has been successful in exploiting low salinity, estuarine habitats (Williams 1974; Norse 1977). In the Middle Atlantic Bight, virtually all postmetamorphic juveniles and adults occupy estuaries and, indeed, penetrate deep into low salinity environments of even large estuaries such as Delaware and Chesapeake bays (Porter 1955; Van Engel 1958). The reproductive phase of the life history, however, retains primitive characteristics, including a requirement for high salinity during the larval stages (Costlow and Bookhout 1959).

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To accommodate this requirement, females migrate to the mouth of the parent estuary after mating. In Chesapeake Bay, this migration can exceed 200 km and results in dense congregations of fertilized females near the Bay mouth during winter (Van Engel 1958). During the subsequent spring and summer, females produce one or two broods, each containing two to three million eggs (Van Engel 1958). Our investigations have centered on the period of the life history between hatching of larvae and their subsequent appearance in the estuary as post-metamorphic juveniles (Sulkin et al. 1980; Epifanio and Dittel 1982; Dittel and Epifanio 1982; Sulkin and Van Heukelem 1982; Epifanio et al. 1984). Given the proximity of the spawning grounds to the estuary mouth and the net seaward flow typical of estuaries of the Middle Atlantic Bight, the potential is high for export of larvae from the site of hatching within the estuary to water of the continental shelf. Direction of initial transport of zoeae immediately after hatching will determine whether larval development will occur within the parent estuary or in waters of the continental shelf.

Our initial investigations therefore have addressed the question of retention versus export of larvae; specifically, what is the horizontal and vertical distribution of the hatching stage and are there adaptations that promote estuarine retention in the face of obvious potential for export of larvae to shelf waters.

Retention Versus Export of Larvae

Chesapeake and Delaware bays are partially stratified estuaries with well-developed density driven, two layer circulation (Boicourt 1981, 1982). Consequently, residual flow at the surface is seaward, while that at depth is landward. Superimposed upon residual circulation are tidal currents and episodic wind-driven events.

The vertical distribution of Stage I *C. sapidus* zoeae thus is likely to be important in determining the direction of initial transport with respect to the parent estuary. Early larval stages of many invertebrate taxa, including brachyurans, possess behavioral adaptations that promote movement to surface water (Thorson 1950, 1964; Sulkin 1984). If *C. sapidus* larvae show such behavioral traits, movement to surface water in Chesapeake and Delaware bays will enhance significantly the probability of their rapid export from the estuary. On the other hand, if retention within the parent estuary is a characteristic of the *C. sapidus* life cycle, early stage larvae should exhibit behavior that results in *avoidance* of surface water.

Sulkin (1984) suggested that adaptations regulating vertical movement of larvae be evaluated with respect to their modifying influence on negative buoyancy. Conservative stimuli effecting orientation (geotaxis) and level of locomotor activity (barokinesis) are particularly important. Sulkin et al. (1980) measured geotactic response of stage I *C. sapidus* zoeae in three salinities. Groups of sibling larvae were placed at one end of a horizontally oriented tank and at the bottom end of a vertically oriented tank. Change in distribution after 30 min in darkness was compared between the two tanks (Fig. 1). Movement along the axis of the horizontal chamber is the consequence of non-oriented (random) movement from the initial point source (section 1). Movement along the axis of the vertically oriented chamber is the result of non-oriented swimming plus swimming that is oriented in response to gravity. In the vertically oriented chamber virtually all larvae moved to the top within 30 min, clearly establishing the role of oriented response. This indicates a negative geotaxis that is pervasive among larvae within all samples tested and forms the basis of upward movement depending upon the rate of locomotion. Sulkin et al. (1980) also demonstrated that swimming speed of Stage I zoeae increased as hydrostatic pressure increased above increments of one atmosphere (high barokinesis). This combination of responses should promote upward movement and maintenance of position high in the water column. Level of locomotor activity in response to more variable stimuli such as salinity and temperature complement geotaxis and barokinesis (Sulkin et al. 1980). Furthermore, sharp vertical salinity (Sulkin and Van Heukelem 1982) or temperature (McConnaughey and Sulkin 1984) gradients should not inhibit upward migration. The hatching stage thus exhibits behavioral traits that should promote movement towards the surface, as is typical with other invertebrate larvae.

This prediction has been confirmed for Delaware Bay by Epifanio et al. (1984), who reported that over 90% of Stage I larvae caught at the mouth were either in the neuston (36.7%) or the top 2 m of the water column (54.2%). Similar results have been reported for Chesapeake Bay (Sandifer 1975; Goy 1976; Provenzano et al. 1983).

Provenzano et al. (1983) suggested that hatching in *C. sapidus* occurs synchronously on night-time high slack tides, a conclusion based on the results of four sampling programs at the mouth of Chesapeake Bay. In all four cases, peaks of abundance of larvae occurred on ebbing tides at night. This observation is confirmed by Epifanio et al. (1984), who also reported peaks of abundance of Stage I zoeae on ebbing tides at the mouth of Delaware Bay. A similar pattern of release of larvae with respect to diel and tidal cycles has been reported for *Uca* sp. (DeCoursey 1979, 1983; Bergin 1981). Christy and Stancyk (1982) suggested that such traits are related to maximum transport from the estuary to the coastal ocean.

Thus, *C. sapidus* exhibits adaptations that exploit both residual circulation and tidal currents such that seaward transport immediately upon hatching is

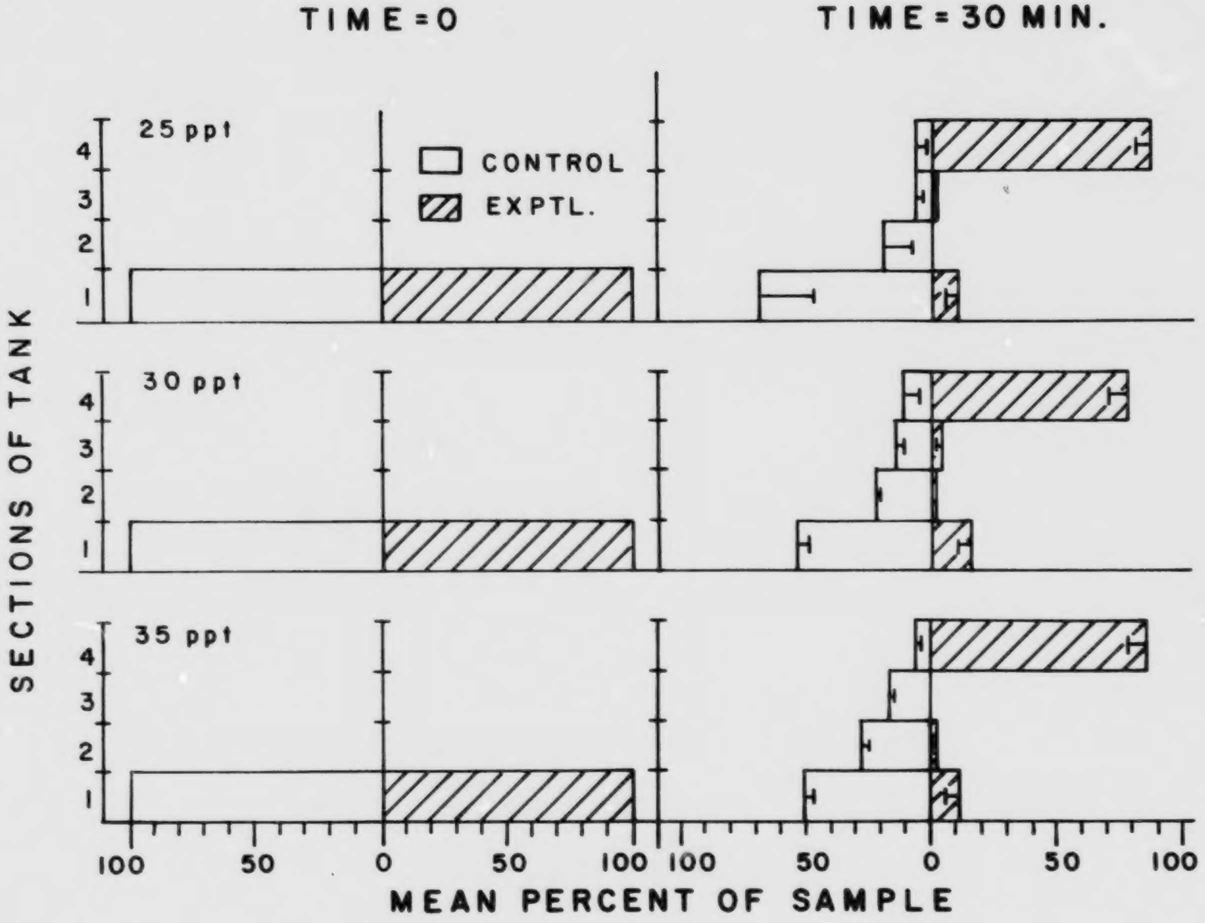

FIG. 1. Response of Stage I *C. sapidus* larvae to gravity in each of the three indicated salinities. Control measures movement in a horizontally oriented tank in darkness; experimental, movement in a vertically oriented tank in darkness. (Adapted from Sulkin et al. 1980.) Section 1 in each case refers to section at end of horizontal tank and at bottom of vertical tank into which larvae are initially placed. Shown are the mean values of nine replicates (30 ppt). T bars represent one standard error.

promoted. Export — rather than retention — is thus assured. The effectiveness of the phenomenon is illustrated by the absence of late zoeal stages (Stages V to VII) in these two large estuaries. Provenzano et al. (1983) reported that more than 99% of *C. sapidus* zoeae captured were of the first zoeal stage. The remainder were Stages II and III. Sandifer (1975) reported that early zoeal stages and a few megalopae were present at the mouth of Chesapeake Bay, but no zoeal stages past the fourth instar were present. Epifanio et al. (1984) reported that all zoeae captured in Delaware Bay were Stage I.

It is therefore apparent that the presence of *C. sapidus* larvae in shelf waters does not represent wastage of offspring from the parent population. Indeed, the evidence indicates that *C. sapidus* larvae are exported to shelf waters where zoeal and megalopa development occur. The fate of these larvae will depend upon biotic sources of mortality present on the shelf and upon dispersal that will be controlled by coastal circulation.

Larval Dispersal in Shelf Water

Contrary to the predictions of Sulkin et al. (1980) that behavioral changes during zoeal development should promote deeper distribution as ontogeny proceeds, the vast majority of zoeae of all stages appear to frequent surface water (Smyth 1980; Johnson 1983; J. McConaugha, pers. comm.; C.E. Epifanio, unpublished data). Their dispersion from the point of export at the estuary mouth will be determined by coastal surface currents.

A proposed model for coastal surface circulation is shown schematically in Fig. 2 (after Boicourt 1982). At the mouth of Chesapeake Bay, and to a lesser extent Delaware Bay, low salinity surface water flows seaward and towards the south along the coast in a characteristic plume (Boicourt 1982). Seaward of the plume, the shelf is characterized by an outer shelf region in which summer circulation, dominated by longshore pressure

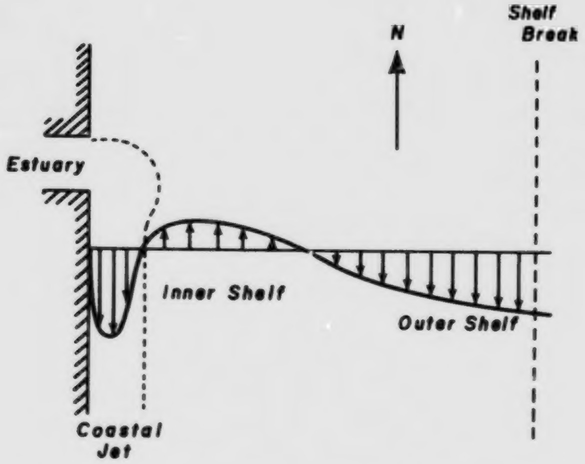

FIG. 2. Schematic alongshore surface velocity profile for summer southern Middle Atlantic Bight (after Boicourt 1982, fig. 6).

gradients and relatively independent of wind stress, exhibits mean southward flow. A more shallow inner shelf region, however, is more sensitive to episodic wind events, and the prevailing southwesterly winds of the summer can dominate the flow (Boicourt 1982). Flow reversal (northerly) can thus occur in a band along the coastline. The timing, size, and persistence of this band depend upon salinity differences between the estuarine plume and inner shelf water, the flux of outflowing water, and the strength and persistence of southwesterlies.

Because vast numbers of larvae will be entrained in southward flowing estuarine plumes and shelf water, there exists the potential for substantial loss of larvae from the Middle Atlantic Bight as these currents become entrained in the Gulf Stream at nearby Cape Hatteras. Indeed, maintenance of substantial numbers of larvae in the Middle Atlantic Bight likely will depend upon flow reversal of inner shelf water.

Ultimately, the size of the pool of potential recruits present in shelf waters will be controlled by both biotic and abiotic factors. Biotic factors such as predation and food availability often are invoked as sources of mortality that may be density-dependent (Ricker 1954; Nelson et al. 1976). By contrast, physical factors cause a constant rate of mortality (or loss from the system) regardless of the numbers of larvae present. Circulation patterns of the Middle Atlantic Bight thus serve as a source of density-independent loss.

Two factors thus determine the number of larvae that will contribute to the pool of potential recruits; namely, level of larval production (a function of spawning stock size) and degree of retention of larvae controlled by shelf circulation. Because these two phenomena will vary independently with time and because the consequences of the presence or absence of favorable circulation in a given year are likely to be profound while those due to annual variations in spawning stock size may be more subtle due to the tremendous fecundity of *C. sapidus*, we propose that year-to-year variation in size of the pool of recruits will depend largely on the presence, timing, and extent of flow reversal on the shelf. This phenomenon thus should be a major factor in regulating recruitment success to Middle Atlantic Bight estuaries.

Onshore Transport of Larvae and Post-Larvae

While the size of the pool of potential recruits present in the shelf waters of the Middle Atlantic Bight obviously contributes to year-class strength, recruitment success ultimately requires transport of offspring from shelf waters to the estuary. Larval transport again will be determined by the interaction between spatial distribution of larvae and shelf water hydrodynamics.

Deep shelf currents exhibit onshore drift, with evidence of convergence at the mouths of major estuaries (Norcross and Stanley 1967; Scheltema 1975). Scheltema (1975) has invoked such residual circulation as a mechanism for transport of *C. sapidus* megalopae to the estuary. However, the vast majority of zoeae and megalopae are present at the surface (Smyth 1980; Johnson 1983).

Johnson (1983) has provided the most comprehensive description of megalopa distribution. He reported the maximum density to be in surface water 33 km offshore, with only 17% of the total captured within Chesapeake Bay. Although most megalopae were captured in surface waters, 12–25% typically were captured near the bottom. Johnson (1983) asserts that megalopae cannot be subject to a conservative transport mechanism via deep residual circulation, but are dependent upon wind-driven onshore flow of surface water. Onshore wind-driven surface flow has been reported for the region in late summer or autumn (Bumpus 1969, 1973; Boicourt 1973; Wang and Elliott 1978). According to this model, recruitment to the estuary from the offshore pool of larvae will be dominated by fortuitous, episodic climatic events.

We suggest an alternative model entirely consistent with the data presented by Johnson (1983). The key is in the characterization of the 12–25% of megalopae that were consistently present near the bottom. If these postlarvae represent the results of random vertical movement of negatively buoyant animals, net directional transport will not be significant. If, on the other hand, megalopae are initially distributed in surface water, reflecting the surface distribution of late zoeal stages (Smyth 1980) but systematically move to deeper water as metamorphosis approaches, a major fraction of surviving megalopae consistently will become entrained in shoreward residual circulation. The result will be a conservative onshore transport mechanism.

Sulkin and Van Heukelem (1982) reported that young megalopae exhibit behavioral traits that promote high precision in depth regulation and upward movement. However, position in the water column will be controlled by level of locomotor response. Systematic movement to deeper water thus could be effected solely by decrease in locomotor activity as metamorphosis approaches. Furthermore Costlow (1967) has reported that the combination of low temperature and high salinity, typical of conditions found at depth on the shelf, will delay metamorphosis. If postlarvae present at depth are in advanced stage of development, the sharp drop in incidence of megalopae within the Bay mouth is explained by a high frequency of metamorphosis as this group of advanced-stage megalopae encounter warmer, less saline water of the estuary. Thus, although an instantaneous measurement of vertical distribution of megalopae on the shelf may indicate that a large majority are at the surface, a conservative deep water onshore transport mechanism may nevertheless exist.

Furthermore, once near the estuary mouth, megalopae may be exploiting tidal currents to increase the probability of their transport into the estuary. Epifanio et al. (1984) reported that megalopae were virtually absent from the water column during ebbing tide, but were found concentrated at various depths during flooding tide (Fig. 3). Transport into the estuary would be enhanced if megalopae, having reached relatively shallow regions near the estuary mouth, remain on the bottom during ebbing tide and rise in concert into the water column on flooding tides. A phenomenon such as this is consistent with reports that megalopae swarm at discrete depths (Chace and Barnish 1976; Rice and Kristensen 1982). Furthermore Sulkin and Van Heukelem (1982) have described behavioral responses of *C. sapidus* megalopae that could account for precise depth regulation and have suggested that vertical location of resulting swarms could be determined by level of locomotor activity regulated by periodic stimuli.

The dominant mechanism for onshore transport clearly remains to be described. Three general alternatives must be considered: (1) shoreward transport is strictly a passive process dependent upon fortuitous wind events, (2) conservative mechanisms are at work resulting from behavioral adaptations of megalopae that exploit residual circulation, and (3) a combination of active (conservative) and passive (episodic) processes occurs. We suggest that the last alternative is the most likely and that co-occurrence between appropriate circulation and availability of megalopae will be a second significant factor contributing to relative recruitment success.

Consequence of Recruitment Model to Sampling and Management Activity

Acknowledging that biotic sources of mortality during larval development will contribute to the level of recruitment success, we propose that the major factors regulating year-to-year variation in year-class strength are physical, hydrographic ones; namely, flow reversal in summer and onshore surface flow in fall timed to enhance conservative mechanisms governing megalopa recruitment. Under these circumstances, it seems likely that predictive models can be developed. Such models must await calibration of wind events with characteristics of shelf circulation and a better understanding of the relationship between active and passive components of shoreward dispersal.

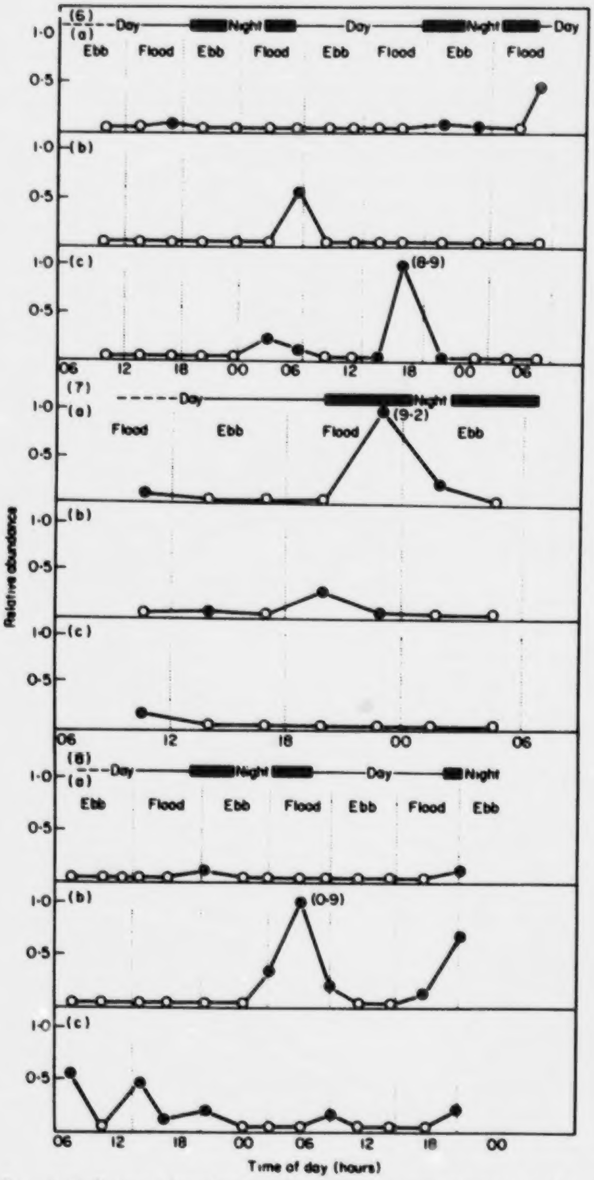

FIG. 3. Relative abundance of *C. sapidus* megalopae in the mouth of Delaware Bay. Samples labelled as (6) were collected on Sept. 3-5, 1980; (7), Sept. 11-12, 1980; (8), Sept. 10-11, 1981. Values in parentheses are the number of megalopae per cubic metre in sample (on each date) containing greatest abundance of megalopae. Open circles represent a relative abundance of zero. (a) relative abundance in neuston layer, (b) relative abundance in surface water (2 m below surface), (c) relative abundance in bottom water (2 m above bottom). (After Epifanio et al. 1984, fig. 6-8).

Because of the nature of the factors that dominate the recruitment process, measurements of larval abundance on the shelf are unlikely to provide useful predictive information, nor are estimates of spawning stock size. The earliest point in the life history providing a reliable measure of year-class strength is the appearance of post-metamorphic juveniles in the lower estuary.

Clearly temporal and spatial vagaries of abundance of juveniles and adults in the estuary will be related to the hydrographic processes that regulate recruitment. The characteristics of flow reversal in a given year, for example, will determine relative annual recruitment success in estuaries from Cape Cod to Chesapeake Bay. One would expect recruitment to the northernmost estuaries within the system to be more highly variable and particularly dependent upon strong flow reversal. Furthermore, it is reasonable to speculate that relative recruitment success north and south of Cape Hatteras may be affected by flow characteristics on the shelf north of Cape Hatteras.

Understanding more fully the physical processes at work in the region and how behavioral adaptations exploit these processes will be essential in describing the mechanism of recruitment in sufficient detail to permit early prediction of year-class strength and to guide consequent management activity.

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POPULATION DYNAMICS

Implications of Size and Sex Regulations for the Lobster Fishery of the Bay of Fundy and Southwestern Nova Scotia

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CAMPBELL, A. 1986. Implications of size and sex regulations for the lobster fishery of the Bay of Fundy and southwestern Nova Scotia, p. 126–132. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

The fishery for the American lobster (*Homarus americanus*) from the Bay of Fundy and southwestern Nova Scotia is briefly reviewed. A yield- and egg-per-recruit model is used to examine the effect of size (minimum and maximum) and sex (protection of ovigerous females) regulations on the dynamics of this lobster fishery. Substantial reductions in fishing mortality from current levels would be required to maximize yield per recruit with the present recruit size of 81 mm carapace length (CL). Increase in recruit size would increase yield per recruit, but application of a 127 mm CL maximum size regulation to protect larger, highly fecund lobsters, concurrent with the present recruit size, would reduce yield per recruit slightly. A maximum size regulation, increases in recruit size and reduction in fishing mortality would substantially increase eggs per recruit. Removal of berried female protection would reduce yield per recruit only slightly, but would substantially lower eggs per recruit irrespective of whether or not a 127 mm CL maximum size regulation existed. Increasing the recruit size by one molt increment and maintaining the protection of berried females are the most effective size and sex regulation options in terms of increasing both yield and eggs per recruit, especially in this area where the current recruit size is about one molt below onset of egg production. As an interim measure, however, adding a maximum size regulation would protect mature females from increasing exploitation while management attempts are made to reduce fishing mortality and to increase the recruit size to a sufficient level.

L'auteur fait un bref examen de la pêche du homard d'Amérique (*Homarus americanus*) de la baie de Fundy et du sud-ouest de la Nouvelle-Écosse. Un modèle du rendement et du nombre d'œufs par recrue sert à l'étude des effets de la réglementation visant la taille (minimale et maximale) et le sexe (protection des femelles ovigères) sur la dynamique de cette pêche. Il serait nécessaire de réduire de façon appréciable les taux actuels de mortalité due à la pêche pour maximiser le rendement par recrue si l'on conservait la taille de recrue actuelle qui est de 81 mm de longueur de carapace (LC). L'augmentation de la taille de recrue se traduirait par une augmentation du rendement par recrue, mais une réglementation limitant la taille maximale à 127 mm de LC afin de protéger les homards plus gros à fécondité élevée abaisserait légèrement le rendement par recrue si l'on maintenait la taille actuelle de la recrue. Une taille maximale réglementée, une augmentation de la taille de recrue et une réduction de la mortalité due à la pêche se traduiraient par une augmentation appréciable du nombre d'œufs par recrue. L'élimination de la protection des femelles œuvées ne provoquerait qu'une légère réduction du rendement par recrue, mais le nombre d'œufs par recrue diminuerait de façon appréciable qu'il y ait ou non réglementation de la taille maximale à 127 mm de LC. L'augmentation de la taille de recrue d'une mue et le maintien de la protection des femelles œuvées constituent les options de réglementation de la taille et du sexe les plus efficaces du point de vue de l'accroissement du rendement et du nombre d'œufs par recrue, surtout dans cette région où la taille actuelle de recrue se situe à environ une mue avant le début de la production des œufs. On pourrait cependant, comme mesure provisoire, imposer une taille maximale afin de protéger les femelles matures d'une plus grande exploitation tout en tentant de prendre des mesures de gestion pour réduire la mortalité due à la pêche et accroître la taille de recrue à un niveau suffisant.

Introduction

One of the most valuable fisheries in Canada is that for the American lobster (*Homarus americanus*). Landings of lobster in Canada during 1982 were about 22 784 t valued at $112.7 million (Fisheries Statistics, Halifax). During 1982, Bay of Fundy and inshore and offshore southwestern Nova Scotia lobster landings (5299 t) and value ($35.3 million) were 23 and 31%, respectively, of the Canadian total. Lobsters in this general area are probably part of one stock (for review, see Campbell and Mohn 1983). During the past decade, increased fishing effort for offshore lobsters (Stasko and Pye 1980; Pezzack and Duggan 1983) and large mature lobsters in the Bay of Fundy (Campbell and Duggan 1980; Campbell 1984), concurrent with high exploitation rates in the inshore fishery of southwestern Nova Scotia (Paloheimo 1963; Campbell 1980), has caused concern to biologists that fishery-caused recruitment failure could occur (Anthony and Caddy 1980; Campbell and Robinson 1983).

Little is known about lobster stock-recruitment relationships in the northern Gulf of Maine (Stasko and Campbell 1980). However, of interest to management of this lobster stock are the biological implications of possible changes in various size and sex regulations on yield- and egg-per-recruit analyses. Yield per recruit (Thomas 1973; Caddy 1977; Ennis 1980; Fogarty 1980; Fogarty et al. 1982; Campbell 1985) and eggs per recruit (Saila and Flowers 1965; Campbell and Robinson 1983; Campbell 1985; Ennis 1985) for *H. americanus* have been estimated for a number of areas. These studies recommended reductions in fishing mortality and increases in recruit size to increase both yield and eggs per recruit to enhance lobster stocks.

Simulation studies of the pros and cons of protecting (ovigerous) berried females have been carried out on New England *H. americanus* (Saila and Flowers 1965) and on United Kingdom *H. gammarus* (Bennett and Edwards 1981). However, there have been no previous studies on the effects of protecting berried female lobsters on yield and eggs per recruit for *H. americanus* from the northern Gulf of Maine. The present paper briefly describes the lobster fishery and examines in detail the effect of: (1) changing recruit size and (2) establishing a maximum size regulation in conjunction with and without the protection of berried females on yield and eggs per recruit under different fishing mortalities for lobsters of the Bay of Fundy and southwestern Nova Scotia.

Description of the Fishery

The inshore lobster trap fishery of the Bay of Fundy and southwestern Nova Scotia is regulated in a number of ways. Although the number of licenses (1465 during 1982) and traps per fisherman (300–375 traps per fisherman) have been limited in recent years, egg-bearing females have been protected and size limits and fishing season restrictions have been imposed since 1873 in all areas. The open fishing season has basically remained fall–spring since the turn of the century with few modifications. The closed summer fishing seasons were intended, in part, to protect lobsters while molting, mating, and extruding and hatching eggs, to reduce exploitation rates, and to adjust for seasonal marketing problems. Size regulations have varied since the turn of the century (Campbell and Duggan 1980; Stasko and Campbell 1980) but, for the last 33 yr, the minimum size limit (recruit size) has been 81 mm carapace length (CL). During the late 1930's, a 127 mm CL maximum size was introduced in Grand Manan (Campbell and Duggan 1980) to coincide with the maximum size regulation of the State of Maine, USA, but it was dropped by 1942. The maximum size regulation, still in place in the State of Maine, is intended to protect large, mature lobsters above 127 mm CL.

The Canadian offshore (greater than 93 km from shore) lobster fishery started in 1971. Regulations include a limit of eight licensed boats, 1000 traps per boat, a 3-mo closure (chosen by fishermen), an annual quota of 408 t for boats fishing only in the Browns Bank area, and a closed refuge area for brood stock on Browns Bank; there is no quota for boats fishing on Georges Bank (Pezzack and Duggan 1983).

Annual inshore landings for the Bay of Fundy and southwestern Nova Scotia have been relatively stable from 1943 to 1982, averaging about 4470 t (± 107 SE). Landings for the Canadian lobster offshore fleet were 461 t (including Browns Bank and Georges Bank) in 1982.

In shallow waters (<70 m) off southern Grand Manan and inshore areas off southwestern Nova Scotia, the mean size of lobsters caught in commercial traps was 80 mm CL (range 60–140 mm CL) (Campbell and Duggan 1980; Stasko and Campbell 1980). In contrast, few lobsters were caught below 90 mm CL (range 65–230 mm CL) off northern Grand Manan, in the upper reaches of the Bay of Fundy (Campbell 1984) and on Browns Bank and Georges Bank (Pezzack and Duggan 1983).

Methodology

The empirical yield and egg-per-recruit model developed for the American lobster by Caddy (1977, 1979) and later modified by Campbell and Robinson (1983) and Campbell (1985) was used to determine the yield and number of eggs produced by 1000 recruits entering a fishery under a range of fishing mortalities and recruit sizes. The growth, reproductive and survival rates used in the model have been described elsewhere (Campbell 1983; Campbell and Robinson 1983; Campbell 1985). The effects of increasing recruit size from 68 to 140 mm CL and/or adding a maximum size regulation (127 mm CL) on yield and eggs per recruit under various instantaneous fishing mortalities ($F = 0.0\text{–}2.6$) were examined with this model. To achieve a maximum size effect, the vulnerability to fishing was set at 1.0 from the recruit size to 127 mm CL then to zero for sizes greater than 127 mm CL. For the simulation runs with unprotected berried females, the model was modified so that the berried females were subjected to the same fishing mortality rates as the non-berried females. Based on analyses of size frequencies, catch-per-unit-effort, and tag-recapture data, the mean fishing mortality for the area was assumed as $F = 1.4$ (range 0.43–1.92) (Paloheimo 1963; Campbell 1980; Campbell and Duggan 1980). Natural mortality was set at $M = 0.1$ (Thomas 1973) for all the simulations.

There are a number of assumptions in the model, such as constant natural and fishing mortalities for all size groups which are discussed in Campbell and Robinson (1983) and Campbell (1985). Although there are simplifications in lobster molt and egg extrusion sequences, an egg-extrusion factor incorporated in the model (Campbell 1985) makes the model versatile in accommodating factors such as one molt-egg extrusion in the same year and multiple egg extrusions within one intermolt period longer than 2 yr (Aiken and Waddy 1980) depending on the specific biology of lobsters in any particular area. Intermolt periods can extend to more than 4 yr in large females (Campbell 1983). In the present paper, the value of all mature females extruding eggs (extrusion factor) was assumed to be half the intermolt period and increased up to about 1.7 for females as large as 170 mm CL (Campbell 1985). The effect of multiple extrusions is negligible (< 2% in eggs per recruit) compared with simulations with only one extrusion per intermolt period at the current recruit size and $F \geq 1.0$. In contrast, adding a maximum size of 127 mm CL, the effect of multiple extrusions increases eggs per recruit by 16 to 11% over single extrusions per intermolt at $F = 0.1$ to 2.6 (Campbell 1985). The maximum size limit protects females that have escaped the fishery from additional F, allowing multiple extrusions amongst the surviving mature females.

Results

YIELD PER RECRUIT

Although the general pattern of yield per recruit at different fishing mortalities was similar for male and female lobsters, yield per recruit for males was 2–3% higher than for females at $F = 1.0$–2.6 and 25% higher at the maximum yield per recruit at the current recruit size of 81 mm (Fig. 1). These differences are due to the higher growth rates of males than females (Campbell 1983). Large reductions of fishing mortality from the current assumed value of $F = 1.4$ would be necessary to maximize yield per recruit at the current size of 81 mm. Decreasing F from 1.4 to 1.0 would increase yield per recruit by 5.9 and 6.6% for females and males, respectively, whereas reductions of F to lower levels (< 0.8) would dramatically increase yield per recruit under present regulations (Fig. 1). Increases in recruit size influence yield per recruit more than changes in fishing mortality when F is greater than 1.0 (Fig. 1, Table 1). Increasing recruit size from 81 to 94 mm, for example (when $F = 1.4$), would increase yield per recruit by 30.5 and 35.5% for female and male lobsters, respectively (Fig. 1, Table 1).

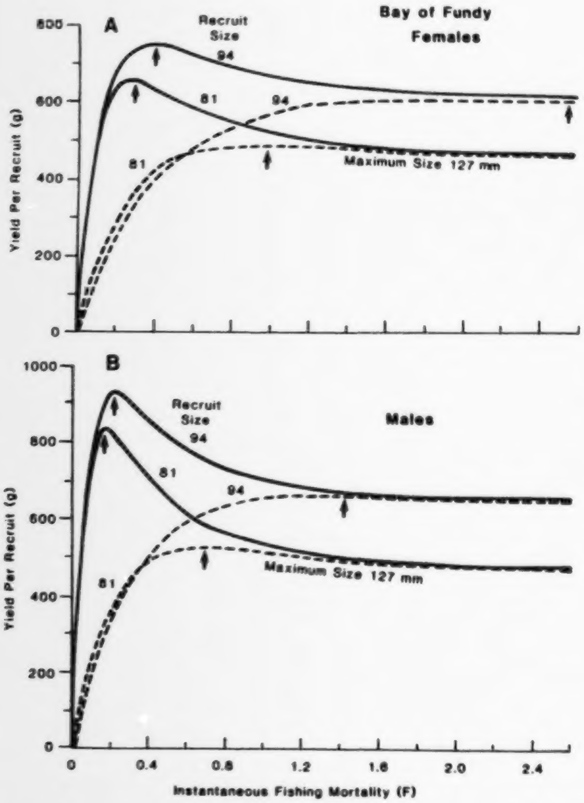

FIG. 1. Relationship between fishing mortality and estimated yield per recruit at two recruit sizes (81 and 94 mm CL) and with (dashed line) and without (solid line) a 127 mm CL maximum size regulation on (A) female and (B) male lobsters from the Bay of Fundy and southwestern Nova Scotia. Arrow indicates fishing level at which yield is maximum. Berried females protected.

TABLE 1. Percentage change in yield and eggs per recruit from the current recruit size of 81 mm CL to various increases (mm) in recruit size, using a 127 mm CL maximum size regulation, or when the protection of berried females (B♀) is removed for lobsters from the Bay of Fundy and southwestern Nova Scotia. Values in brackets are yield (g) or number of eggs per recruit at current recruit size with or without 127 mm CL maximum size at natural mortality $M = 0.1$ and fishing mortality $F = 1.4$. Percentage change = $((y/x) - 1.0) \times 100$ where x = yield or eggs per recruit at current recruit size, and y = yield or eggs per recruit at changed size in same column.

Recruit size	Male Yield	Female (B♀ protected)		Female (B♀ not protected)	
		Yield	Eggs	Yield	Eggs
		Without maximum size			
81	(502)	(489)	(352)	(485)	(126)
85	10.0	9.5	125.1	8.7	132.5
90	23.4	21.3	281.6	19.5	298.2
94	35.5	30.5	416.0	28.2	430.0
		With 127 maximum size			
81	(499)	(482)	(1440)	(484)	(311)
85	10.2	7.5	126.3	8.4	134.7
90	22.9	16.8	284.1	18.9	303.2
94	33.1	24.9	419.8	27.2	437.9

The introduction of a maximum size of 127 mm CL to the current recruit size of 81 mm CL would result in similar values of yield per recruit as would the current recruit size alone for $F > 1.2$ (Fig. 1); however, the peak at $F < 1.0$ would be removed. There is a slight reduction (−0.07 and −1.4%) for both males and females in yield per recruit when adding a maximum size regulation for $F > 1.2$ (Fig. 1, Table 1). Yield-per-recruit values of males and females, with and without a maximum size, diverge as the recruit size increases, especially above 90 mm CL since the fishable size range becomes smaller; yield-per-recruit values with an upper maximum size start to decline rather than increase at about 105 mm CL (Fig. 2, Table 1).

Removal of protection for berried females from fishing mortality would result in only a minor reduction (−0.1 to −2.6%) in yield per recruit at recruit sizes up to 94 mm CL with no maximum size and with fishing mortality ranging from $F = 1.4$ to 2.0 (e.g. Fig. 2, Table 1). Increasing recruit size with no maximum size resulted in lower yield-per-recruit values for unpro-

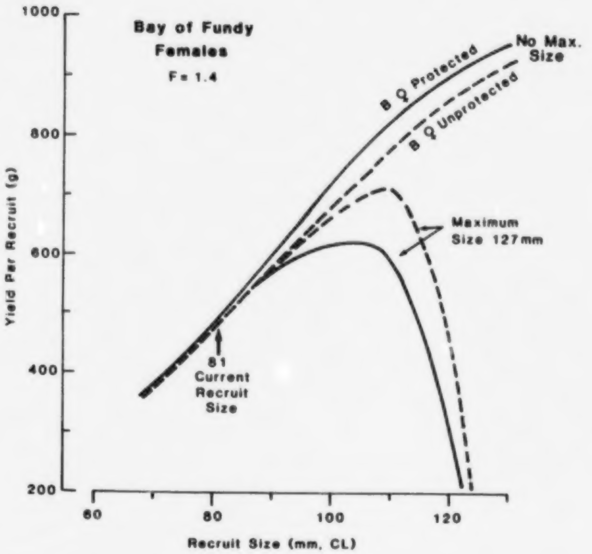

FIG. 2. Relationship between recruit size and estimated yield per recruit for female lobsters with and without a maximum size regulation and with (solid line) and without (dashed line) protection of berried females from fishing mortality in the Bay of Fundy and southwestern Nova Scotia. $F = 1.4$.

tected berried females compared with protected ones (Fig. 2). In contrast, with a maximum size regulation, there was a greater increase in yield per recruit for unprotected versus protected berried females (Fig. 1, Table 1). This is because relatively more lobsters became available to fishing as the size range between recruit size and maximum size became smaller.

EGGS-PER-RECRUIT

The relative numbers of eggs per recruit are sensitive to various fishing mortalities (Fig. 3). Substantially more eggs per recruit would be produced with decreases in fishing mortality; e.g. a 283% increase would result if F was reduced from 1.4 to 1.0 at the current recruit size (Fig. 3). Increasing the recruit size to 94 mm with no maximum size results in an increase (416%) in eggs per recruit (Fig. 3, Table 1).

Adding a 127 mm CL maximum size to 81 and 94 mm CL recruit sizes at $F = 1.4$, increases the eggs per recruit by 309 and 312%, respectively (Fig. 3, Table 1). Although there is a substantial increase in eggs per recruit with a maximum size, the relative changes in eggs per recruit generally parallel those without a maximum size for most F values (Fig. 3, Table 1). For example, increases of recruit size from 81 to 94 mm CL with a maximum size results in slightly higher (419.8%) eggs per recruit than without a maximum size (416%) (Table 1). More eggs per recruit are produced at fishing mortalities of $F \leq 1.2$ with a maximum size regulation and an 81 mm CL recruit size, than with only a recruit-size regulation of 94 mm CL (Fig. 3).

Removal of protection of berried females from fishing mortality would result in substantial reductions (45–78%) in eggs per recruit (Fig. 4, Table 1). Changes in recruit sizes and fishing mortalities resulted in similar relative changes in eggs per recruit with and without berried female protection. At recruit sizes less than 105 mm, no protection of berried females would result in a greater loss in eggs per recruit with a maximum size than without a maximum size regulation in place (Fig. 4,

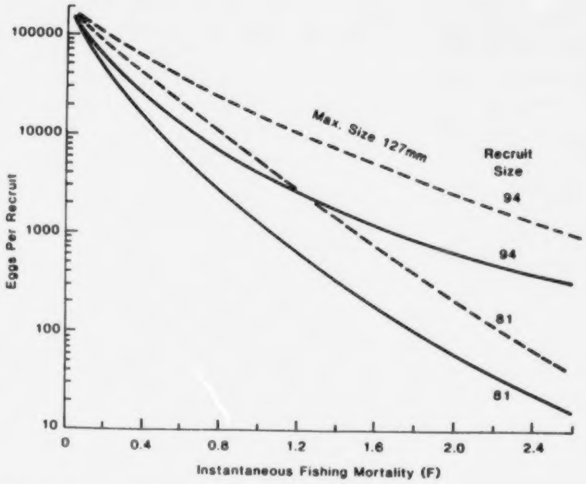

FIG. 3. Estimated eggs per recruit under different fishing mortalities and two recruit sizes (mm CL) with (dashed line) and without (solid line) a maximum size regulation for female lobsters from the Bay of Fundy and southwestern Nova Scotia. Berried females protected.

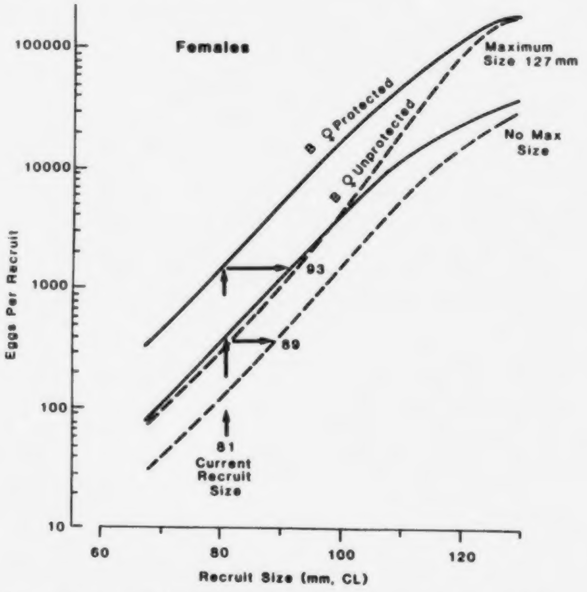

FIG. 4. Relationship between recruit size and estimated eggs per recruit with and without a maximum size regulation and with (solid line) and without (dashed line) protection of berried lobsters from fishing mortality in the Bay of Fundy and southwestern Nova Scotia. Horizontal arrows indicate the recruit size (mm CL) of a female population with unprotected berried females which produce the same number of eggs per recruit as that with protected berried females at the current recruit size of 81 mm. $F = 1.4$.

Table 1). The present recruit size of 81 mm CL would have to be increased to 89 mm CL (no maximum size) and to 93 mm CL (with a maximum size) to produce the equivalent number of eggs per recruit if protection of berried females was removed (Fig. 4).

Discussion

Reductions in fishing mortality and increases in recruit size would benefit the Bay of Fundy and SW Nova Scotia lobster fishery by increasing yield per recruit of males and females and eggs per recruit of females. Although substantial reductions in fishing mortality would be required to maximize yield per recruit, small reductions in fishing mortality would significantly increase eggs per recruit. In addition, even small reductions in effort through reducing fishing season, fishing licenses and the number of traps per boat would be economically beneficial by reducing labor, fuel, and capital costs associated with fishing long seasons and large number of traps (Acheson 1975).

Ideally, most females in a lobster population should be allowed to extrude eggs at least once prior to entering the fishery to reduce the risk of recruitment failure (Anthony and Caddy 1980). However, the size at 50% maturity occurs at about 108 mm CL for female lobsters in this area (Campbell and Robinson 1983) which would require a substantial increase in recruit size. In addition, increasing the recruit size to a level (> 120 mm CL) which would give the maximum yield per recruit at current *F* values would be socially unacceptable. However, increasing the recruit size by one molt increment from 81 to 94 mm is an effective management strategy in terms of both increasing yield and eggs per recruit. Although a 30.5-35.5% increase in yield per recruit for females and males, respectively, would be realized with a recruit size increase of 81-94 mm CL, an abrupt single increase would mean about a 67% loss in catch in the first year in the inshore areas of southwestern Nova Scotia where most lobsters caught are close to recruit size. However, the desired increase could be reached in small increments (e.g. 1 mm per year) over several years (with about 5% loss in catch in the first year although the benefits of increasing recruit size would balance out losses in subsequent years), thereby minimizing any social or economic disruptions that may result. Increasing recruit size from 81 to 94 mm CL in the offshore areas and in the upper reaches of the Bay of Fundy would have a minimal effect since only a few fishermen are involved and their catch consists of mostly lobsters greater than 95 mm CL.

Establishing a maximum size regulation of 127 mm CL with an 81 mm CL recruit size would increase egg production by 309% and have little effect on yield per recruit. Fishermen fishing mainly large lobsters would lose 15-52% of their catch, depending on the area, should a maximum size regulation be enforced. In areas such as in Maine, USA, where a 127 mm CL maximum size regulation is already in place, increases in recruit size would result in similar percentage increases in yield and eggs per recruit as without a maximum size limit (Table 1). However, the starting point in eggs per recruit with a maximum size limit would be higher (by about 309%), than that without a maximum size (Table 1). Consequently, maintaining a 127 mm CL maximum size while increasing recruit size up to about 94 mm CL (Fig. 2) would be advantageous, even at high *F* values (Fig. 3), especially if increasing egg production is an important management strategy. This conclusion is contrary to that of Saila and Flowers (1965) who suggested a maximum size had no biological significance due to the small numbers of mature females remaining in the population after high fishing mortalities.

Protection of berried females increases egg production but has little effect on yield per recruit at a given recruit size up to 94 mm CL (Fig. 2). The results of the present study and those of Saila and Flowers (1965) clearly indicate that egg production with protection of berried females is substantially higher than with no protection. Although the landing of egg-bearing *H. americanus* has been banned in North America, most European countries allow the landing of berried *H. gammarus* (Bennett 1980). The voluntary participation of most fishermen and the method of detecting scrubbed lobsters with staining of the cement on the swimmerets (Karlsson and Sisson 1973) has helped to effectively enforce the protection of berried females in North America. However, because of administrative and enforcement difficulties, regulations for protecting berried females from fishing were dropped in most European countries. Bennett and Edwards (1981) advocated an increase in recruit size to increase yield and eggs per recruit to compensate for the increased fishing mortality and lack of berried female protection to avoid the risk of fishery-induced recruitment failure for European lobster stocks in United Kingdom waters.

Protection of all females would also increase eggs per recruit considerably but reduce yield of females to zero. The latter management strategy could be achieved, where recruitment failure was apparent, by having a male-only fishery, but the resulting disruption of the sex ratio (reductions in available males for mating) may have negative reproductive effects.

Although lobster landings in the Bay of Fundy and SW Nova Scotia have been relatively stable during 1943-82, the recent increases in fishing effort on large lobsters (Anthony and Caddy 1980; Campbell and Duggan 1980; Fogarty et al. 1982) may require some compensatory management strategy to avert a decline in egg production and, consequently, lobster landings. Reductions in fishing mortality, increasing recruit size and/or adding a maximum size would clearly increase egg production substantially. Whether or not increasing egg production would translate into increased recruitment is a matter of speculation since the stock-recruitment relationship for this area is unknown. The shape of the stock-recruitment relationship e.g. a dome-shaped Ricker (1954) or asymptotic Beverton-Holt (1957) or other type curve has not been determined since the brood-stock size and level of recruitment of larvae or juvenile *H. americanus* in this area have been difficult to measure accurately. At present, landings are well below historic levels and with current high fishing mortalities the parent stock size is probably at the low end of the range, suggesting the relationship is on the left-hand or ascending part of the stock-recruitment curve, whatever its shape (Ennis 1985). This assumption suggests that increases in egg production would probably increase recruitment provided there is sufficient habitat carrying capacity. Increases in egg production would also probably ensure stable recruitment by providing a buffer to various mortality factors.

The number of eggs per recruit (352) for the Fundy area seems low compared with that (2420) for the eastern Nova Scotia area predicted by the model at $F = 1.4$ and recruit size of 81 mm CL (Campbell and Robinson 1983). Despite the lower egg production predicted by the model, the Fundy and southwestern Nova Scotia area has maintained relatively productive and stable landings whereas declines in landings in eastern Nova Scotia have occurred. A number of hypotheses have been proposed to explain the decline in landings in eastern Nova Scotia (Dadswell 1979; Robinson 1979; Wharton and Mann 1981; Pringle et al. 1982; Harding et al. 1983). Campbell and Robinson (1983) suggested, for the Fundy area, that this apparent contradiction was due to a large Continental Shelf area of the Gulf of Maine providing sufficient refugia to protect reproductive lobsters from high exploitation (Anthony and Caddy 1980) and with low survival to maturity of inshore lobster populations, the mature lobsters moving to and accumulating in the offshore areas (Campbell and Stasko 1985) may constitute a "refugium" in space that produces larvae contributing to recruitment to the inshore fishery (Stasko 1978). The seasonal movement of mature lobsters into shallow waters during the summer months and deeper waters in the winter months (Campbell 1984) may allow the mature lobsters to escape much of the fall-spring fishing season which would constitute a refugium in time (Anthony and Caddy 1980).

The egg-per-recruit model uses constant size-specific mortality for all size groups and thus can not accurately accommodate the seasonal changes in movement of mature lobsters and the resulting lower fishing mortalities on sizes beyond onset of maturity. However, if a maximum size such as 127 mm CL is added and assumed to act as a "refugium" for larger lobsters, there is a 309% increase (from 352 to 1440) in eggs per recruit for the Fundy area but only an 18.7% increase (from 2420 to 2873) in eggs per recruit for the eastern Nova Scotia area at a recruit size of 81 mm CL and $F = 1.4$. The main reason for this difference is that most eggs per recruit are produced at lobster sizes before the maximum size of 127 mm CL is reached for the east Nova Scotia area compared with those of the Fundy area. The size at maturity is lower and most (> 80%) egg production occurs in the 70 to 100 mm CL range for eastern Nova Scotia compared with the 95 to 140 mm CL range for the Fundy area (Campbell and Robinson 1983; Campbell 1985). The regional comparison emphasizes the important effect of the choice of recruit size and the local size at maturity on the egg-per-recruit simulations. The analyses suggest that a maximum size regulation would benefit the Fundy and southwestern Nova Scotia lobster fishery as an interim measure to protect the reproductive females from increased exploitation, especially if management initiatives to reduce fishing mortalities and to increase the recruit size are difficult to implement as a result of socioeconomic resistance to changes in the conservation regulations.

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Artisanal Fishery and Development of a Data Base for Managing the Loco, *Concholepas concholepas*, Resource in Chile

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CASTILLA, J. C., AND G. JEREZ. 1986. Artisanal fishery and development of a data base for managing the loco, *Concholepas concholepas*, resource in Chile, p. 133–139. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

Concholepas concholepas (Mollusca: Gastropoda: Muricidae), known as loco is heavily exploited in Chile. During the 1982 season the artisanal fishery landed 20 097 t, with a total value of over $32 million (U.S.). Landing statistics for the last 38 yr and current measures to reduce overexploitation of this species are examined.

To aid in formulation of a rational management policy for this important resource, we are developing a data base for the loco fishery that includes information on length composition of the catch and catch-per-unit-effort in several areas of central Chile.

In this paper we discuss the application of cohort analysis for loco stock assessment based on examination of length frequencies, and an estimation of growth parameters. The implication of using this type of analysis for management of the loco fishery in Chile is also discussed.

Concholepas concholepas (Mollusca : Gastropoda : Muricidae) connu sous le nom de loco est fort exploité au Chili. Pendant la saison de 1982, la pêche artisanale a produit 20 097 t, dont la valeur totale dépassait 32 millions de dollars américains. Nous examinons ici les statistiques de débarquement visant les 38 dernières années ainsi que les mesures actuelles pour arrêter la surexploitation de cette espèce.

Afin d'aider à l'élaboration d'une politique rationnelle de gestion pour cette importante ressource, nous sommes en train de mettre sur pied une base de données pour la pêche du loco, qui comprendra des informations concernant la composition de longueur de la prise ainsi que les prises par unité d'effort dans plusieurs régions du centre du Chili.

Le présent document traite de l'application de l'analyse par la cohorte pour l'évaluation des stocks de loco en fonction de l'observation des fréquences de longueur et de l'estimation des paramètres de croissance. Les répercussions qui découleraient de l'emploi de ce genre d'analyse pour la pêche du loco au Chili sont aussi étudiées.

Introduction

Concholepas concholepas (Bruguière, 1789) (Mollusca, Gastropoda, Muricidae) known as loco is a marine gastropod of great economic importance in Chile. Castilla (1982) estimated that the 24 000 t of loco landed in the country in 1980 had a value of over $20 million (U.S.). The species occurs along the coast of Peru and Chile and is harvested by artisanal divers (commonly using "hooka" gear) at depths between 4–25 m. Castilla (1982, 1983) reviewed the literature on the species, most of which pertains to the biology of the animal, taxonomy, anatomy, physiology, behaviour, ecology, bathymetric distribution, migration and life history. A few reports were concerned with preliminary estimations of population parameters such as growth (i.e. Tobella 1975; Acuña and Stuardo 1979; Guisado and Castilla 1983) or refer to the artisanal fishery (i.e. Castilla and Schmiede 1979; Castilla 1982). Papers dealing with population dynamics or management of the fishery are nonexistent. Nonetheless, loco fishery regulations, such as the legal minimum size, have been in operation for the last 20 yr. In 1982 due to initial indications of overexploitation, a 3-mo closed fishing season was enforced. Annual production figures of legal size locos and stock estimates are lacking in the country (Castilla 1982), but there is an urgent need to obtain fisheries biology information and to develop an appropriate statistical data base for the species. The same author showed that analysis of 22 yr of landings was inadequate to reach a decision on future management strategy.

Based upon biological and fisheries information on the species collected during the past 14 yr and in a recent research project (International Development Research Centre, Canada, and Pontificia Universidad Católica de Chile, 3-P-80-0107) two papers were developed for this meeting. The first relates to the fishery, estimation of basic parameters, population dynamics and the practical use of such information on fishery models that are currently available. In the second paper (Geaghan and Castilla 1986) recent experiences in modelling the loco fishery are discussed.

Study Area and Methods

Figure 1 shows the study area and main loco sampling sites. They extend along central and southern

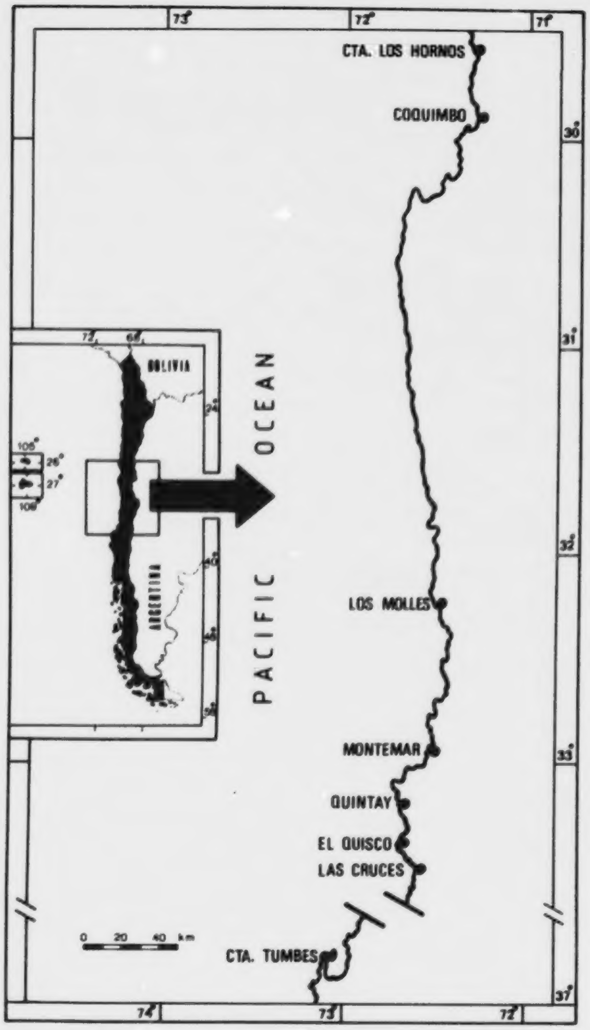

FIG. 1. Study area and main *Concholepas concholepas* sampling sites in Chile.

Chile, from Caleta Hornos 22°54'S, 70°18'W to the Tumbes Peninsula, 36°40'S, 73°07'W. All sampling sites are located in or around traditional loco fishery coves or caletas. In all cases but Tumbes (Acuña and Stuardo, 1979) the loco population structure was determined by three methods: (a) sampling the rocky intertidal zone for periods of 4 h during spring tides by two persons, one a local shellfish collector and the other a scientific investigator; (b) 3-4 h free diving searches by a local loco diver during the same day, from the low water mark to a depth of 4 m; and (c) random sampling of 150-200 locos from commercial catches from the same fishery cove taken on the same or following day.

Maximum shell length and width were measured to the nearest 0.5 mm. Total weight was recorded to the nearest 0.5 g of clean, unfouled shells.

Growth was determined by: (a) examining changes in the length frequency distribution (i.e. Guisado and Castilla 1983) in small intertidal populations; (b) studying modes in length-frequency distribution using the graphical method of Cassie (1954) and Walford regression line equation (Walford 1976) as discussed by Ricker (1975); (c) tagging experiments conducted in Caleta Hornos and Coquimbo, as described by DuBois et al. (1980). A von Bertalanffy growth curve was fitted using the Beverton (1954) method. The instantaneous rate of total mortality ($\hat{\mu}(Z)$) was estimated following the first method described by van Sickle (1977). Other parameters were taken from Geaghan and Castilla (1986). Length composition data from commercial catches were used for stock assessment (Jones 1974, 1981). Regressions were done with the Biomedical Design Program (BMDP) 1R on the DEC 10 (Digital Equipment Corp.) computer.

Results

THE *CONCHOLEPAS* FISHERY AND COLLECTION OF STATISTICAL DATA

Figure 2 shows total landings of *Concholepas* in Chile for the last 38 yr. During the period 1945-74 landings increased steadily from about 1 000 to 6 000 t per year. Between 1975 and 1980 landings increased abruptly reaching a peak of 24 856 t in the last year. Castilla (1982) discussed this situation and showed a close relationship between increased *Concholepas* landings and the opening of international markets, mainly in Japan. In 1981 a regulatory measure came into force and a 3 month closed season was instituted (March 1st-May 31st in northern and central Chile and January 1st-March 31st in the south). This regulatory measure is still (1984) in operation and protects the species from fishing during the critical period of reproduction when they congregate in large numbers (Castilla 1979).

According to the statistics (SERNAP 1982) during 1982, 5 982 t of *C. concholepas* meat (i.e. frozen, canned) was exported with a total value of $26 121 000 (U.S.). The calculated value of the resource consumed in the country is about $6 million (U.S.) per year.

Collection of fishery statistics in Chile is done by the Servicio Nacional de Pesca (SERNAP). Unfortunately

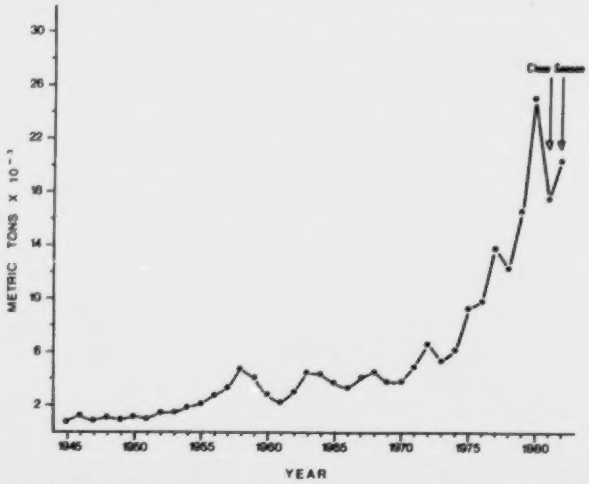

FIG. 2. Artisanal landings of *Concholepas concholepas* (whole weight in tonnes) in Chile between 1945 and 1982.

the available published information on the artisanal fishery is rather incomplete (Castilla 1982). There is good information regarding monthly and yearly landings of shellfish (Castilla and Becerra 1976) for the last 50 yr, but information on effort, number of artisanal boats or amount of diving is scarce. This is not surprising and is the situation in most artisanal or small fisheries throughout the world (Munro 1979; Gulland 1979). In the case of *Concholepas* where no license limitation or limit on effort per boat has ever been imposed, the interpretation of past landing statistics is difficult. For an opposite case see the abalone *Haliotis kamtschtkana* fishery (Breen 1980).

Since 1981 we have been engaged in two pilot artisanal data collecting programs in Chile:

a) Figure 3 shows three traditional loco fishery caletas in central Chile where well defined loco fishing areas are identified. In 1983 we introduced specially designed data collection sheets in Quintay, Algarrobo-El Quisco, and Las Cruces. We have monitored the artisanal activity of those caletas daily on a boat by boat basis. All landed species, particularly loco, have been recorded. Furthermore, randomly selected boats have been used on a monthly basis to obtain length composition data of loco from the commercial fishery.

b) At Cruz Grande, Caleta Hornos and Coquimbo (see Fig. 1) the Servicio Nacional de Pesca (SERNAP) has been recording total catch and effort for the loco fishery on a daily basis since 1981. No length composition data were recorded there. Fishery statistics on loco landings and effort derived from these pilot programs have been used in this paper and in Geaghan and Castilla (1986).

GROWTH, CRITICAL SIZE, AND MINIMUM SIZE FOR FISHERY

Maximum shell length and width and shell length against total animal weight relationships were investigated previously for use in morphometric or gravimetric parameters in growth models. Locos sampled in Caleta Hornos in June 1984 were used. For the length-width relationship we found the following relationship:

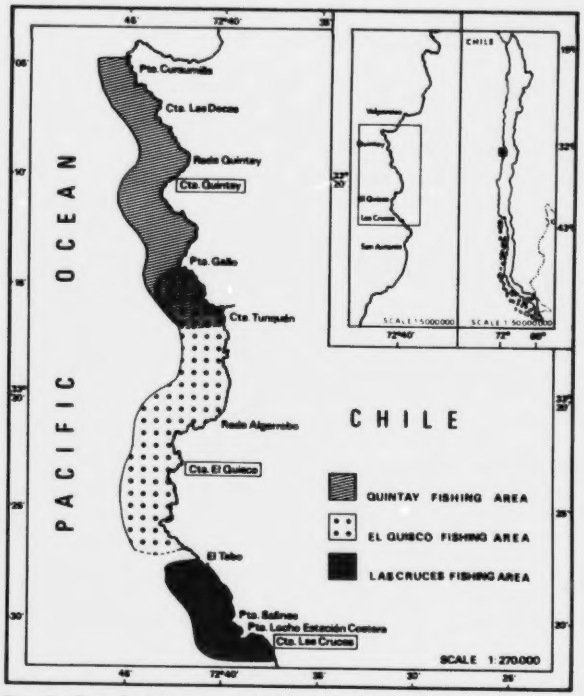

FIG. 3. *Concholepas concholepas* fishing areas of Quintay, El Quisco-Algarrobo and Las Cruces.

$$\text{Width} = 0.597 \times \text{Length}^{1.052}, \ (n=112, r^2=0.989)$$

For the length-weight relationship ($w=al^b$) we found:

$$\text{Weight} = 6.567 \times 10^{-5} \times \text{Length}^{3.265}, \ (n=112, r^2=0.992).$$

As discussed by Ricker (1975) these functional regression values describe an isometric growth pattern for *Concholepas*. Table 1 shows the estimates of von

TABLE 1. *Concholepas concholepas*. Estimation of von Bertalanffy growth parameter calculated using Ford-Walford lineal equation (see Ricker 1975), first step, and Beverton (1954) modification.

Geographical locality	Date	Sample n	Asymtotic length L_∞(mm)	Ratio[c] F	Brody coefficient k	Ratio[c] F	Biological zero t_o (yr)	Source[b]
Las Cruces[a]	06/11/83	193	183.098	$P \leq 0.05$	0.203	$P \leq 0.001$	−0.023	DIUC
Las Cruces[a]	07/09/83	166	167.150	$P \leq 0.001$	0.215	$P \leq 0.001$	−0.012	DIUC
El Quisco[a]	02/15/84	606	172.534	$P \leq 0.08$	0.229	$P \leq 0.05$	−0.014	IDRC/PUC
Quintay	02/22/84	308	168.241	$P \leq 0.05$	0.202	$P \leq 0.001$	−0.035	IDRC/PUC
Grouped data[a]			175.247		0.212		−0.021	
Montemar/Tumbes	10/15/67	105	185.012	$P \leq 0.001$	0.161	$P \leq 0.001$	−0.102	Acuña and Stuardo (1979)

[a] Length frequency distribution method (Cassie 1954). Data from Artisanal Fishery Landings.
[b] J. C. Castilla Research Projects: Dirección Investigación P.U. Católica de Chile (DIUC 42/76); IDRC/PUC 0-80-107.
[c] Probabilities obtained from BMDP1R program using DEC-10 Computer.

TABLE 2. *Concholepas concholepas*. Estimates of *Tmb* and critical size using different values of *M* (see text) and von Bertalanffy growth equation parameters as shown in Table 1.

Localities	Date	Age at critical size, *Tmb* (yr)			Critical size (mm)		
		$M=0.15$	$M=0.20$	$M=0.23$	$M=0.15$	$M=0.20$	$M=0.23$
Las Cruces	06/11/83	7.99	6.88	6.38	140	129	124
Las Cruces	07/09/83	7.76	6.70	6.22	120	120	115
El Quisco	1983-84[a]	7.51	6.50	6.04	136	126	121
Quintay	1983-84[a]	8.01	6.90	6.39	130	120	115
Grouped data		7.82	6.74	6.26	132	124	119

[a] Fishing season 1983-84.

Bertalanffy growth parameters for different population samples. The asymptotic length (L_∞), Brody coefficient (k), and biological zero (t_0) calculated from a group of five samples using the Ford-Walford linear equation (see Ricker 1975, for first step) and Beverton's (1954) modification were used to fit the von Bertalanffy growth equation parameters:

$$L = 175.25\ [1 - e^{-0.212\,(t-(-0.021))}]$$

The age at which *Concholepas* cohorts reach their maximum biomass (critical size) was calculated using the Alverson and Carney (1975) equation:

$$Tmb = [(1/k\ \ell n\ ((M+3k)/M)]$$

Critical size was then calculated from Tmb using von Bertalanffy growth equations. Table 2 shows the results for three geographical localities and grouped data, using three values of the instantaneous rate of natural mortality, M. The value of $M = 0.15$ was estimated for locos harvested at Caleta Quintay after an approximate seven month sampling period (June-December, 1983) by Geaghan and Castilla (1986). The values of $M = 0.20$ and $M = 0.23$ represent estimates of maximum natural mortality in semi-virgin loco populations of Isla Pájaros (IV Region of Chile, about 500 km north of Caleta Quintay).

Table 2 shows that in all cases the critical sizes are above 100 mm maximum shell length, which has been the minimum legal size in the *Concholepas* fishery in the country since 1981. Previous minimum legal sizes (1965-80) were 95 mm in northern Chile and 105 mm in central and southern Chile.

MORTALITY RATE

Table 3 shows estimations of the instantaneous rate of total mortality, $\hat{\mu}(Z)$, following the first method of van Sickle (1977) and using the Brody Coefficient (see Table 1) for four populations sampled along the central coast of Chile. The mean rate of growth, $\hat{g}$, for *Concholepas* was estimated from Fig. 4, derived from the work of Gallardo (1973), Guisado and Castilla (1983), and Castilla (unpublished data). Estimation of the slope, $\hat{s}$, [ln N_S (Z)] was calculated over the size range of interest for each population. It can be seen that the percentage of annual mortality rate for typical loco fishing areas, El Quisco and Quintay, are extremely similar, around 85%.

TABLE 3. *Concholepas concholepas*. Total mortality rate estimated using van Sickle (1977), method N° 1 (equation 5) at different geographical localities of Chile.

Localities	Date	Sample N	Size Range (mm)	Slope[a] $\hat{s}$	Growth[b] $\hat{g}$(mm/yr)	Brody coefficient k	Total mortality rate $\hat{\mu}(z)(yr^{-1})$	Rate of mortality (%) (yr^{-1})
Las Cruces	06/11/83	193	90-125	−0.120	8.95	0.203	1.277	72.1
Las Cruces	07/09/83	166	90-115	−0.179	8.95	0.215	1.817	83.8
El Quisco[c]	1983-84	1120	90-115	−0.193	8.95	0.229	1.956	85.9
Quintay[c]	1983-84	2434	100-135	−0.187	8.95	0.202	1.876	84.7
Montemar/Tumbes	10/15/67[d]	105	96-111	−0.217	8.95	0.161	2.103	87.8

[a] Slope calculated using Histogram length-frequency.
[b] Mean growth rate (see van Sickle 1977), calculated using the upper limit of annual mean growth rate.
[c] Fishing season 1983-84.
[d] Data from Acuña and Stuardo (1979).

CONCHOLEPAS STOCK ASSESSMENT BASED ON COHORT ANALYSIS

Table 4 shows cohort analysis (Jones 1981) based on length composition data for locos in Quintay, between June 1983 and February 1984. The cohort analysis shows the number of locos caught and provides estimates of the average number of locos attaining each length during the sampling period as well as the average number present in a size group at any particular moment. For example 533 997 locos attained a length of 100 mm at some time during that fishing season, and 241 828 were caught. It can be seen that with the actual fishing effort the survival rate (S_t) is rather low, around 0.50 for locos of 100 mm, and that the exploitation rate (F/Z), of about 0.92, is rather high.

In the next section we discuss the validity of extending our calculations to determine the long-term effects of changes in the loco fishery effort either in Caleta Quintay or other localities along Chile.

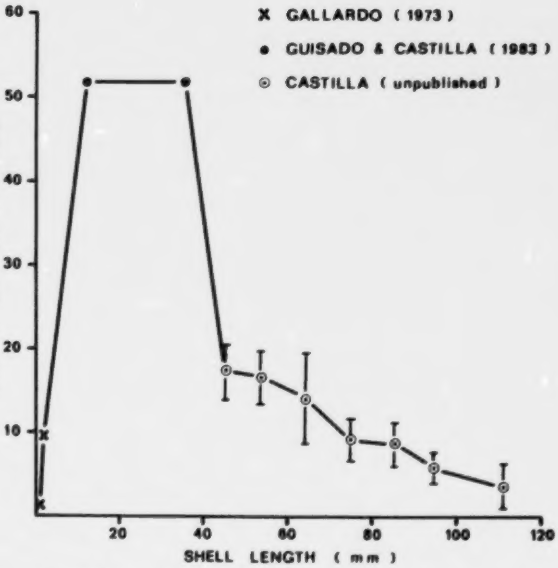

FIG. 4. Growth rate of *Concholepas concholepas* from available data. Curve fitted by eye. Bars show stardard error, $\alpha = 0.05$.

Discussion

The *C. concholepas* fishery is highly important in Chile and perhaps one of the most valuable of its kind in the world. The opening of international markets for the species during the past 10 yr has increased Chilean loco landings approximately 4–6 times over historical figures.

Loco fishery regulations such as legal minimum size have been enforced during the past 20 yr and recently new regulatory steps have been taken. In 1982 a 3-mo closed fishing season was introduced in the country.

We believe the main questions relating to the state of exploitation in this fishery, and the best regulatory measures to be implemented, can only be determined through stock assessment studies. Accordingly, in this paper we present for the first time estimations of the basic population parameters of loco populations in central Chile. These estimates and those calculated by Geaghan and Castilla (1986) have allowed calculation of the critical size of loco in the Caleta Quintay fishery using different estimates of natural mortality. In all cases critical sizes were about 100 mm shell length which is the minimum legal size in the fishery. These results must be validated in the future, particularly through further direct estimations of M. According to Castilla (1979) locos begin to spawn at a size of about 40–50 mm, far below the present legal size. Breen (1980) discussed the danger of lowering minimum legal size to increase yield for *Haliotis kamtschtkana*. Our results (see Table 1) show differences in the von Bertalanffy

TABLE 4. *Concholepas concholepas*. Cohort analysis of the number caught in the various length groups at Caleta Quintay during 1983 fishing season (June 1st, 1983–February 28th, 1984). $L_\infty = 168.4$ mm; $M = 0.15$; $M/k = 0.7426$; F/Z (max. class) $= 0.9200$; $F = 1.726$; $k = 0.2020$ (see Table 1; Geaghan and Castilla 1986 and text).

Classes length (mm)	*XL*	Number sampled	Number caught	Number in year class	*ST* = EXP(−*ZT*)	*ZT*	*F/Z*	*FT*	*Z*	Average number in sea	*DT* (yr)
7.00–7.50	1.020	0	0	906921.100	0	0	0	0	0	0	0
7.50–8.00	1.021	0	0	872472.042	0	0	0	0	0	0	0
8.00–8.50	1.022	0	0	837544.703	0	0	0	0	0	0	0
8.50–9.00	1.023	0	0	802104.780	0	0	0	0	0	0	0
9.00–9.50	1.025	32.00	8588.79	766113.287	0.94130	0.06049	0.191	0.01155	0.1854	242534.136	0.326
9.50–10.00	1.027	575.00	154329.86	721144.374	0.74049	0.30045	0.825	0.24776	0.8554	218784.153	0.351
10.00–10.50	1.029	901.00	241828.18	533996.893	0.50491	0.68337	0.915	0.65509	1.7588	150314.588	0.389
10.50–11.00	1.031	550.00	147619.86	169621.527	0.40979	0.89218	0.928	0.82759	2.0720	76807.120	0.431
11.00–11.50	1.034	220.00	59047.95	110480.594	0.41870	0.87060	0.919	0.80045	1.8618	34495.065	0.468
11.50–12.00	1.037	86.00	23082.38	46258.389	0.44850	0.80186	0.905	0.72550	1.5752	16195.578	0.509
12.00–12.50	1.041	43.00	11541.19	20746.674	0.38800	0.94675	0.909	0.86057	1.6479	7704.951	0.575
12.50–13.00	1.046	17.00	4562.80	8049.741	0.37147	0.99028	0.902	0.89306	1.5280	3311.163	0.648
13.00–13.50	1.053	6.00	1610.40	1990.271	0.39023	0.94101	0.883	0.83110	1.2842	1419.808	0.733
13.50–	—	4.00	1073.60	1166.901			0.920				
Total		2434.00	653285.0	5899611.276						751566.550	

growth parameter estimated in different populations studied. There are differences in growth rate and L_∞ between populations. Sainsbury (1982a,b) found similar results for the paua *Haliotis iris* in New Zealand. Therefore, the use of "grouped growth data" (see Table 1) as proposed in this paper, must be regarded as tentative. Further, as discussed by Sainsbury (1980), the effect of individual variability on the von Bertalanffy growth equation should be investigated in loco. The use of length composition data (Jones 1974, 1981) as a method to assess stocks that does not require age data, could be useful as a first approach, but may be unsuited to species that exhibit a high degree of individual variability in growth (Sainsbury 1982b).

In spite of the limitations mentioned above we feel confident of growth parameters used in this study. For instance, our calculation of L_∞ for Quintay 168.241 mm, or for "grouped data," 175.247 mm (see Table 1) agrees with the largest loco, 161 mm recorded in Quintay, or for that matter from all the localities from Las Cruces to Coquimbo during the study. The largest known loco is a specimen reported from Taltal, northern Chile, of 179 mm (J.C.C. collection).

Estimates of Brody's coefficient (k) reported here are similar to those calculated by Miranda (unpublished report to Subsecretaría de Pesca, Chile, 1980) for the same species. They are rather smaller than those calculated for herbivorous gastropods, such as abalone (i.e. Breen 1980). Perhaps, one would predict smaller M values for a high trophic level carnivorous species such as *C. concholepas*.

The preliminary results of the VPA Jones cohort analysis model (1974, 1981, see Table 4) cannot be fully analysed at present. For length cohort analysis it is assumed that input length composition is representative of a steady state situation. A useful approximation would be the determination of the average length composition over a period of as many years as possible. Since we do not have sufficient data, we cannot extend our calculations. Meanwhile, estimates for survival rate of locos above legal size appear rather low and exploitation rates and total mortality are high. Results for the 1984-85 loco fishing season will be used to validate stock assessment estimates here and explore long-term efects of changes in loco fishing effort in central Chile.

Authors' Note

Since preparation of this paper (1983) a closed season was instituted on harvest of loco for a 2-yr period (March 1985-87) in the northern region of Chile, from approximately north of Caleta los Hornos to the border of Peru. The regulation was introduced because of reported overexploitation of stocks and the effects of the most recent El Niño phenomenon.

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Population Dynamics of the Dungeness Crab (*Cancer magister*)

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BOTSFORD, L. W. 1986. Population dynamics of the Dungeness crab (*Cancer magister*), p. 140–153. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

Although Dungeness crab (*Cancer magister*) catch records exhibit considerable interannual fluctuations throughout its range (central California to Alaska), most research has been on cyclic variations along northern California, Oregon, and Washington. Three categories of mechanisms have been proposed as explanations of observed cycles. The first, a predator-prey mechanism, has been discounted for both man and adult chinook salmon (*Oncorhynchus tshawytscha*) as predators. The second category, density-dependent recruitment, has been studied by developing mathematical population models, determining conditions necessary to cause cycles in these models, then testing proposed mechanisms against these conditions. Cannibalism and density-dependent fecundity or larval survival remain as possible causal mechanisms, but an egg-predator worm has been discounted as the sole cause of the cycles. Mechanisms in the third category, environmental forcing, have been evaluated by computing correlations between environmental variables and catch records. Upwelling during spring and summer was discounted as the cause of cycles because it did not appear to be cyclic. Southward winds during the late larval period (spring) have been shown to be both correlated with catch several years later and cyclic. Combined effects of the latter two categories, density-dependent recruitment and environmental forcing, are evaluated here through simulation. Results show that a linear effect of spring winds on recruitment could not cause the observed catch record and that either a nonlinear effect of wind or density-dependent recruitment (or both) may be involved. Knowing which mechanism is causing the cycles is important for fishery management because removal of adults affects recruitment differently for each mechanism. Management should take these differences as well as the remaining uncertainties into account. Further progress in understanding these cycles will require direct sampling of larval and post-settlement phases, along with measurement of oceanographic conditions. Mechanisms proposed for Dungeness crab are related to similar mechanisms proposed for other crustacean species.

Bien que les prises de crabe dormeur (*Cancer magister*) présentent des variations interannuelles importantes dans toute sa zone de distribution (du centre de la Californie à l'Alaska), la plus grande partie des recherches a porté sur les variations cycliques des prises sur les côtes du nord de la Californie, de l'Oregon et de Washington. Trois catégories de mécanismes ont été proposées pour expliquer les cycles observés. La première, des mécanismes prédateur-proie selon lesquels les prédateurs seraient l'homme ou le saumon quinnat adulte (*Oncorhynchus tshawytscha*), a été écartée. La deuxième catégorie de mécanismes, soit le recrutement en fonction de la densité, a été étudiée par l'élaboration de modèles mathématiques de la population, la détermination des conditions nécessaires à la création de cycles dans ces modèles et la vérification des mécanismes proposés en fonction de ces conditions. Le cannibalisme et la fécondité ou survie des larves en fonction de la densité pourraient expliquer certaines des variations, mais la prédation des œufs par un ver a été éliminée comme cause unique des cycles. Les mécanismes de la troisième catégorie, soit de forçage environnemental, ont été évalués par le calcul de corrélations entre les variations environnementales et les prises. Parce qu'elles ne semblent pas cycliques, les remontées d'eau au printemps et en été ont été écartées comme facteur responsable des variations. On a montré qu'il existe des corrélations entre les vents printaniers dirigés vers le sud durant la fin de la période larvaire et les prises quelques années plus tard, et que ces vents semblent cycliques. Nous évaluons ici, par simulation, les effets combinés du recrutement en fonction de la densité et du forçage environnemental. Les résultats montrent qu'un effet linéaire des vents printaniers sur le recrutement ne pourrait être à l'origine des prises observées et que l'explication pourrait être soit un effet non linéaire du vent, soit le recrutement en fonction de la densité, ou encore les deux. Pour la gestion des pêches, il est important de connaître le mécanisme responsable des cycles étant donné que la prise d'adultes modifie de façon différente le recrutement selon le mécanisme en cause. Les gestionnaires doivent considérer ces différences ainsi que toutes les incertitudes qui restent. Pour mieux comprendre ces cycles, il faudra échantillonner directement les phases larvaires installées au fond, et mesurer les conditions océanographiques. Les mécanismes proposés pour le crabe dormeur sont liés à des mécanismes semblables proposés pour d'autres espèces de crustacés.

Introduction

Although the range of the Dungeness crab (*Cancer magister*) extends from central California to Alaska, research on population dynamics has focused on more southerly populations. The central California stock is of interest because of its collapse in the late 1950's (Wild and Tasto 1983 and references therein), while stocks from northern California to Washington have attracted considerable research attention because of their approximately cyclic covariation (Fig. 1). For a variety of possible reasons, catch records along British Columbia and Alaska have not exhibited this unusual behavior. Although the focus here is on cyclic popula-

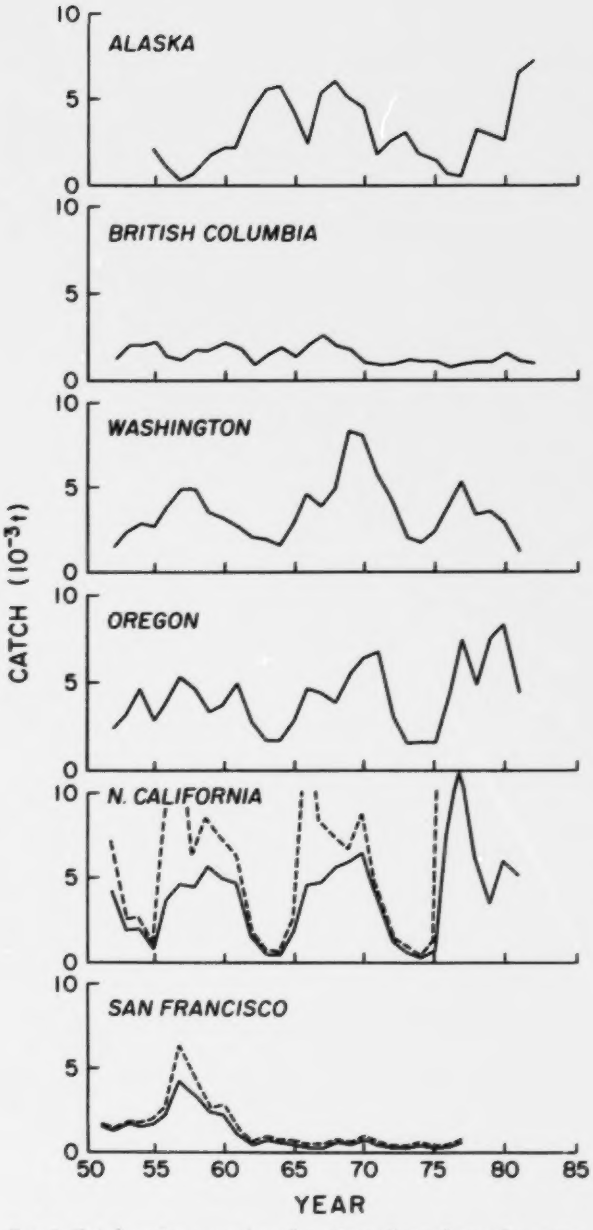

FIG. 1. Catch series at various locations throughout the range of the Dungeness crab. Dashed lines are estimates of preseason abundance (Methot and Botsford 1982, points shown as offscale were extremely high but their abundance could not be estimated.). Only males greater than a certain carapace width are legally taken, except in British Columbia.

tions, much of what we have learned about them may be valuable in investigations of other Dungeness crab populations.

Three categories of mechanisms have been proposed as the cause of these cycles: (1) predator-prey interactions, (2) density-dependent recruitment, and (3) cyclic environmental variables. Our research on this species over the past ten years can be viewed as an attempt to disprove various hypothetical mechanisms within each of these classes. Evidence relevant to each proposed mechanism is reviewed here. The possibility that the cause of cycles involves a combination of mechanisms from both the second and third category is then evaluated. Most of this work has focused on northern California but the results are relevant to cyclically varying Dungeness crab stocks off Oregon and Washington.

Predator-Prey Interactions

Two potential mechanisms in the predator-prey category have been discounted. To test the possibility that man as a predator was causing the cycles, Botsford et al. (1983) analyzed catch, abundance and effort data to determine whether relationships between predator and prey required for cycles in a predator-prey system were present. Although the required lag between changes in abundance and subsequent changes in effort is present, the required influence of a decline in effort on the subsequent increase in abundance is not (i.e., an increase in abundance does not appear to be the result of a decline in effort). A second possible predator-prey interaction is predation by chinook salmon (*Oncorhynchus tshawytscha*) on crab megalopae. Although the catch record for this species is also cyclic with the same period as the crab, the phase relationship implied by larval predation does not match lags actually seen (Botsford et al. 1982).

Density-Dependent Recruitment

Density-dependent recruitment has long been known to be a potential cause of cycles in recruitment (Ricker 1954), and there are several density-dependent recruitment mechanisms in Dungeness crab populations. To test whether one or more of these density-dependent recruitment mechanisms could actually cause the observed cycles we needed to know which characteristics of density-dependent recruitment processes cause cycles. We therefore formulated a mathematical population model that included density-dependent recruitment and age structure, and analyzed stability characteristics of this model.

The model represented recruitment rate as the product of total population reproductive rate and a survival function that depends on effective population size.

$$(1) \quad R_t = B_t f[C_t] \qquad 0 \leq f|C_t| \leq 1$$

where R_t = recruitment rate
B_t = total population reproductive rate
C_t = effective population size
$f|\cdot|$ = recruitment survival function

Total reproductive rate was the sum over the number of females at each age times their fecundity.

$$(2) \quad B_t = \sum_{a=0}^{\infty} n_{a,t} b_a$$

where $n_{a,t}$ = number at age a, time t
b_a = fecundity at age a

Effective population size was similar except the weighing function c_a replaced b_a.

$$(3) \quad C_t = \sum_{a=0}^{\infty} n_{a,t} c_a$$

where c_a = relative effect of an individual of age a on density-dependent recruitment

Thus, this model represents the age-specific effect of older individuals on recruitment in terms of both reproduction and density-dependent recruitment. Note that this differs from the usual stock-recruitment formulation in that effects of the population on reproduction and density-dependent recruitment are represented separately by different functions. Because of this, the effect of an individual on density-dependent recruitment need not be the same as its effect on fecundity.

Analysis of the stability characteristics of this model led to formulation of two characteristics of density-dependent recruitment mechanisms that cause cycles in recruitment. These could both be compared to field and fishery data. The first was that the period of cycles was approximately twice the mean time lag between the age at which density-dependent recruitment is manifested in young and the age at which density-dependent recruitment is caused by older individuals. This result had been obtained earlier through simulation (Ricker 1954).

The second result was a stability condition that involved only two population parameters. This result enabled us to determine whether a mechanism could cause population cycles, by comparing values of two population parameters. One of these parameters reflects the destabilizing ability of the recruitment survival function and the other represents stability inherent in the age structure of the population. The first, termed K, is the slope of the stock-recruitment survival function f at equilibrium (Fig. 2a). As that (negative) slope becomes steeper, the mechanism becomes more destabilizing and more likely to cause cycles. Whether the population actually becomes cyclic depends, however, on whether the value of K is less than the second parameter, termed K'. This parameter depends on how the age structure of the population affects density-dependent recruitment. Usually (but not always), a broad flat age structure ($K' << -1$) is more stable than a narrower one ($K' < -1$) and the least stable form is that analyzed by Ricker (1954), a single reproducing age class ($K = -1$) (Fig. 2b). Note that this implies that intense size selective fishing can make a population less stable, a new conclusion (Botsford and Wickham 1978; c.f. Ricker 1954).

With these two results in hand we began to collect data on potential density-dependent recruitment mechanisms so that we could test whether they could possibly cause the observed cycles. Essentially, we sought the information necessary to compute the expected period of cycles and the values of K and K' for each potential mechanism. However, before we could use these modeling results to confidently reject potential mechanisms we needed to examine the sensitivity of our results to various model assumptions and increase the realism of the model where possible.

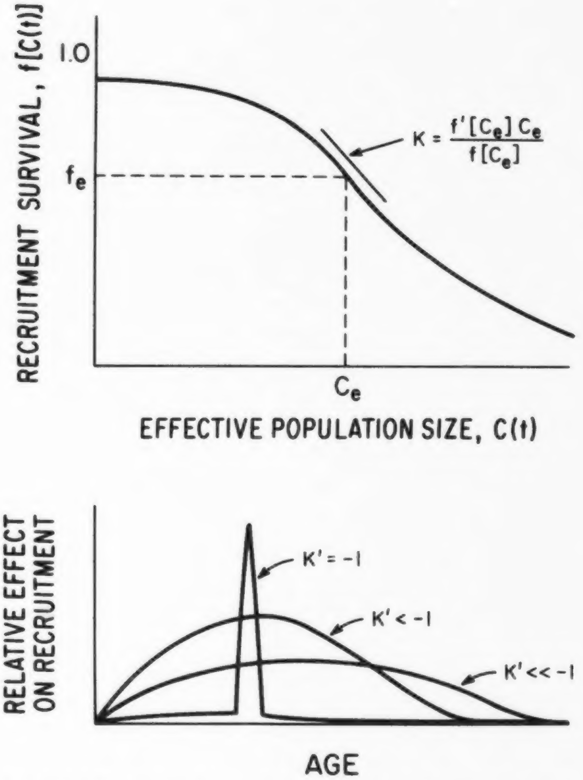

FIG. 2. (a) The dependence of survival to recruitment on adult population size, and the definition of K, the normalized slope of this function at equilibrium. (b) The effect of age structure $|(\text{survival to age } a) \times c_a|$ on the stability limit of K (K').

One of the assumptions inherent in an age-structured model is that a cohort is either completely in the fishable stock or not in the fishable stock. As can be seen in Fig. 3, this is not the case for this species. Individual cohorts appear to enter the fishable range of sizes (i.e., greater than 159 mm) over ages (from hatch) 3 yr (approximately 10%), 4 yr (approximately 40%), 5 yr (approximately 40%) and 6 yr (approximately 10%) (Botsford 1984). The effect of increasing the realism of our model by adding the size distribution of each cohort is shown in Fig. 4. For the former, age-structured model with individuals entering the fishery at age 4 yr, both the period and the stability decline with increasing harvest as described above. When size structure is added, individuals enter at ages 4 and 5 yr. Inherent population stability does not change appreciably, but the period of cycles increases. For this example, parameter values that could correspond to cannibalism as the density-dependent recruitment mechanism were used (i.e., we assume that an individual's cannibalism rate is a constant fraction of metabolic demand, hence the weighting function c_a in equation (3) is proportional to metabolic rate, weight to the 0.8 power). However, the direction and magnitude of changes would be similar for other mechanisms.

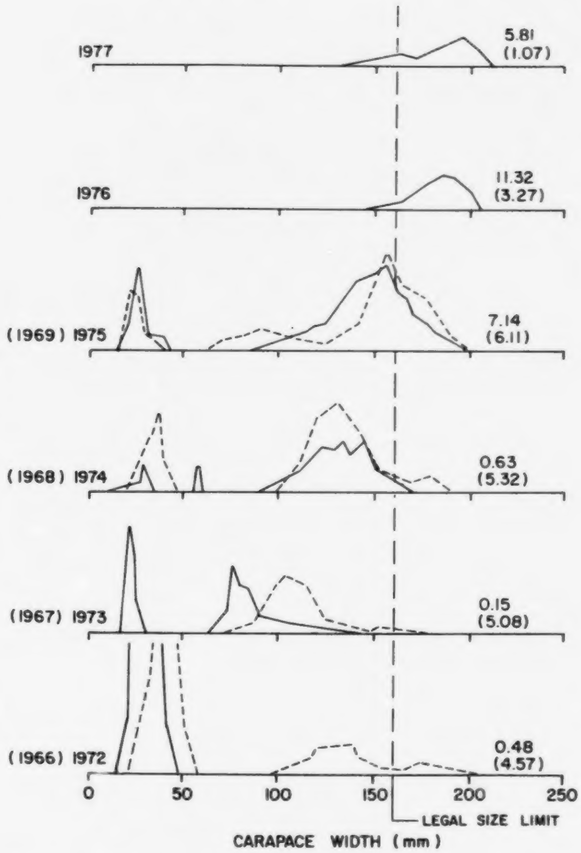

FIG. 3. Size distributions from November cruises by the California Department of Fish and Game show recruitment of two cohorts, 1972 (solid curve) and 1966 (broken curve) into the fishery over several years. Total catch in the commercial fishery (10^{-3}t) for the fishing season following the sample (December–June) is listed to the right of each plot (1966–69 in parentheses). Data for 1976 and 1977 were collected using commercial traps, hence are biased to sizes greater than 150 mm. Data for earlier years were collected by trawl. Because of changes in sampling procedures, vertical scales are not necesarily the same for each year (from Botsford 1984).

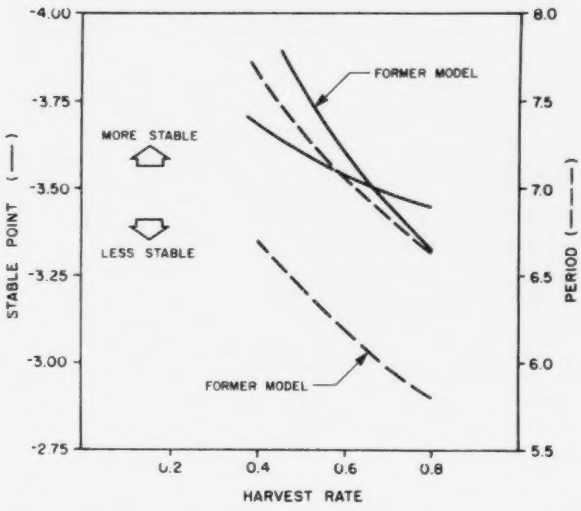

FIG. 4. Changes in stable point (*K'*) and period of cycles as harvest rate changes for the age-structured model (former model) and the size-structured model (from Botsford 1984).

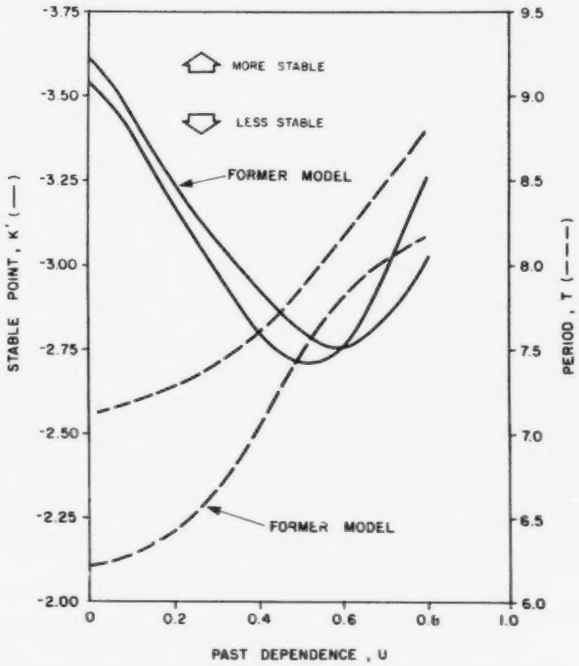

FIG. 5. Changes in stable point (*K'*) and period of cycles as lagged effort increases for the age-structured model (former model) and the size-structured model (from Botsford et al. 1983).

A second critical assumption in the original model was that of constant harvest rate from year to year. Subsequent estimates of abundance (Fig. 1, Methot and Botsford 1982) obtained through the Leslie depletion method revealed that harvest rate was low in the first high years of a cycle and high in the first low years of a cycle. This implied a lagged response of effort to abundance. The effect of adding a lagged response of strength *U* is shown in Fig. 5 (Botsford et al. 1983). As the strength of the lagged response of effort to abundance increases, stability first decreases, then increases. The period of cycles increases with increasing lagged effort response. Again, parameter values used here are those used above for cannibalism as the density-dependent mechanism, but the direction and magnitude of changes would be similar for other parameter values.

We can compare these results regarding stability and period of the cycles with extant data on each mechanism to determine whether that mechanism could be causing the cycles. However, rejection of one of these potential causes must be qualified. Additional departures from reality may still exist in the model from which the stability criteria and period of the cycles were derived, and one or more of them may inadvertently be responsible for rejection of a hypothesis (Botsford 1981b).

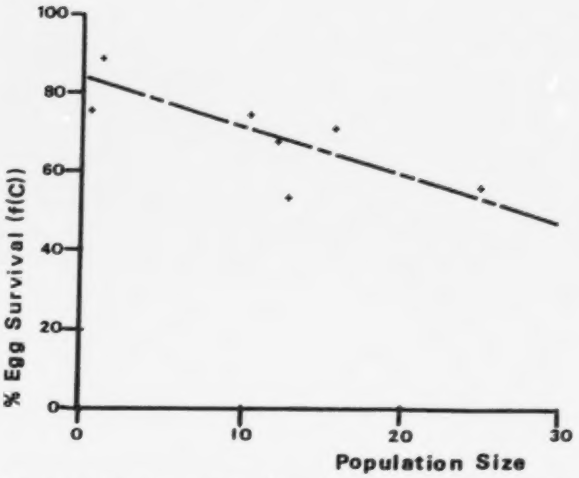

FIG. 6. A plot of recruitment survival (1 − fraction of eggs eaten) versus effective population size [taken here to be catch in the previous year (10^{-3}t)] for the egg predator mechanism. The value of *K* [see Fig. 2(a)] varies with assumed equilibrium level but is near −0.3 (Data from D.E. Wickham).

One proposed mechanism is an egg-predator worm *Carcinonemertes errans*, (Wickham 1978). Although this is actually a predator–prey interaction rather than density-dependent recruitment, it can be viewed as density-dependent recruitment if crab egg mortality depends on crab fecundity, either in the previous or in the same year. The expected period is about 10 or 12 yr depending on whether the lag of 1 yr is used. From data collected by D. Wickham in northern California over the past several years (Fig. 6), survival declined with increasing population size (taken here to be proportional to catch), but the value of *K* appears to be only about −0.3 (this value varies slightly with the assumptions used to compute population size, Hobbs and Botsford, unpublished ms.). From analysis described above, the population would be stable for values of *K* greater than −1.0. Therefore, it is not likely that the egg-predator worm is the sole cause of the cycles. However this mechanism is present in the population and may contribute to cyclic behavior in concert with another density-dependent or environmental mechanism.

A second mechanism, cannibalism, was proposed by Winnor (1966) and Botsford and Wickham (1975). The existence of widespread cannibalism in this species has been implied primarily on the basis of gut contents (Butler 1954; Gotshall 1977; Stevens et al. 1982). We have been collecting crabs for gut content analysis for the past several years but have not been able to estimate *K* and *K'*. Estimating *K* is more difficult for cannibalism than for the egg predator because of difficulties in determining actual mortality rates for cannibalism. With regard to *K'*, our assumption that cannibalism is proportional to weight to the 0.8 power implies most cannibalism is by older individuals. Our gut content data from transects off Eureka, California show cannibalism by adults up to 160 mm carapace width. However, inside estuaries, both our data and those of Stevens et al. 1982 show considerable cannibalism on young-of-the-year by 1-yr-olds. Since cannibalism by 1-yr-olds would tend to stabilize the population and any cycles would be of period 2 yr, if cannibalism in the estuary is a significant part of total cannibalism in the population, cannibalism would not be a likely cause of cycles. This underscores the importance of an outstanding question in Dungeness crab ecology, the relative importance of estuaries versus the outer coastal areas as juvenile nurseries (Tasto 1979; Stevens and Armstrong 1984).

Computations of expected period have thus far been based on the assumption that c_a is the weight at age a to the 0.8 power (i.e., proportional to metabolic requirements). From Fig. 4 this period is between 7 and 9 yr, a value slightly lower than the period of observed cycles. This disparity was pointed out by Botsford and Wickham (1978) (their table 2) for the original version of this model. However, because of the many unverified assumptions made in development of the model they did not reject cannibalism on this basis. Both improvements in the model (realistic growth rates and effort response) have indicated a longer expected period. It should be pointed out that there is not complete agreement on this issue. McKelvey et al. (1980) developed a similar model of the crab population and obtained the same result, that the period of cycles using parameters for cannibalism was lower than the observed period. They, however, rejected the cannibalism hypothesis on that basis (Botsford 1981b; McKelvey and Hankin 1981).

The cannibalism hypothesis is a complex issue, but rejection of cannibalism as a cause of cycles does not currently appear justifiable. Although computed periods are lower than observed (Botsford and Wickham 1978), much of the biology in the model is still based on assumptions rather than data. The combination of cannibalism and the current model can be rejected, but cannibalism in general can not. Cannibalism may not function in the way in which it is currently expressed in the model. For example, in assuming that cannibalism is proportional to metabolic rate represented by weight to the 0.8 power for both males and females we are omitting the metabolic energy expended by females each year in egg production. In fish, that can be as much as 50% of total metabolic input (LeCren 1962). Addition of this consideration to the model would increase the expected period further.

A third mechanism, some form of density-dependent natality or larval survival, was proposed on the basis of a model in which density-dependent recruitment depended on females only (McKelvey et al. 1980). Since females are not fished (hence live longer) and the density-dependent recruitment occurs at a younger age (pre-settlement versus post-settlement), the lag between them is longer than for a mechanism such as cannibalism. As a result, the period expected from this type of mechanism would be greater, near 10 or 11 yr. With regard to the potential for unstable behavior, since this mechanism has not been shown to exist it is difficult to determine how it varies from year to year (i.e., the value of *K*). However, other considerations cast doubt on its being the causal mechanism. First, because the slope of the recruitment survival function must be less than −1.0 to cause cycles, the mechanism must be of the over-compensatory or Ricker type (Ricker 1954) rather than the compensatory or Beverton–Holt type (Beverton and Holt 1957). Since density-dependent larval survival would be "density" rather than "stock" dependent (*sensu* Harris 1975), it is not likely to be of the over-compensatory or Ricker-type. A Beverton-Holt relationship appears to be more likely than a Ricker type for density-dependent fecundity also (Harris 1975; Cushing and Horwood 1977). However, for another crustacean, *Panulirus cygnus*, a dome-shaped relationship between spawning stock and settlement of the puerulus stage has been observed (Morgan et al. 1982). A second characteristic that renders this mechanism an unlikely cause is the dependence of recruitment on female crabs only. Density-dependent fecundity is generally thought to be food-related. Because the proposed model requires dependence of recruitment on females only, it would require a separate food resource for males and females.

Environmental Forcing

On the basis of the strong covariation in catch records along the coasts of California, Washington and Oregon the Pacific Marine Fisheries Commission (1965) proposed a coastwide, environmental factor as the mechanism driving the cycles. Direct effects of temperatures and salinity were evaluated in the laboratory, but the range of these variables seen in nature was deemed insufficient to cause substantial larval mortality (Reed 1969). Shortly after Bakun's development of an upwelling index (Bakun 1973), Peterson (1973) examined the possibility that upwelling over the spring and summer months was driving the cycles in crab catch in northern California, Oregon and Washington. On the basis of a significant relationship between upwelling averaged over spring and summer, and crab catch 0.5 and 1.5 yr later he concluded that upwelling was driving the observed cycles. As noted by Peterson (1973), this conclusion was somewhat dissatisfying because of the short lags involved. A lag of less than 3 yr precludes an effect of environment on the larval phase.

Botsford and Wickham (1975) examined the same data using techniques from time series analysis. They also obtained a significant cross correlation at low lags (Fig. 7). However, while the autocorrelation of catch indicated a cyclic process (i.e. a decline to a negative value then an increase to a positive value at a lag equal to the period), the autocorrelation of upwelling did not. These are shown for northern California in Fig. 7, and results were similar for Oregon and Washington. They therefore concluded that although upwelling may influence crab catch in the following couple of years it was not driving the cycles in the sense that cycles in catch were following cycles in upwelling.

Wild (1980) noted that troughs in the northern California catch record corresponded to peaks in the local winter sea surface temperatures (Fig. 8). The proposed mechanism was a deleterious effect of warmer water on egg development. Computation of correlations show that this temperature series is not cyclic and correlation between the two series is not significant. Woelke (1971) found Dungeness crab landings in Washington during the period 1947–63 to be inversely correlated with deviations from long-term average sea temperatures 4 yr earlier.

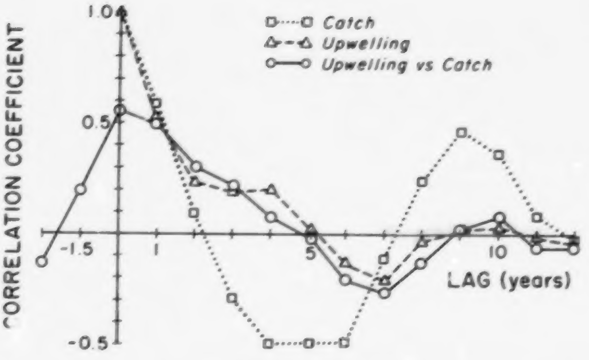

FIG. 7. The cross-correlation between upwelling index and crab catch, the autocorrelation of upwelling index, and the autocorrelation of crab catch for northern California (redrawn from Botsford and Wickham 1975).

Love and Westphal (1983) noted the close correspondence between the sunspot data and total crab catch along the west coast of North America (Fig. 8). They computed significant correlations between the two series for each of the two cycles (1955–64 and 1965–75) separately. Note that these two series are in phase in the 1950s and crab catch appears to lead sunspots in the 1970's as would be expected from the cycles in sunspots having a period of 11 yr and the cycles in catch 10 yr.

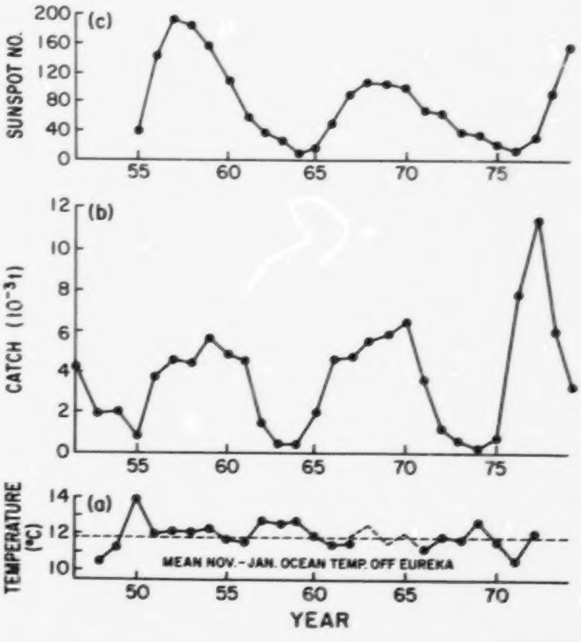

FIG. 8. A comparison of crab catch in northern California (b) and sea surface temperature 4 yr earlier (a) (redrawn from Wild 1980), along with sunspot numbers (c) (redrawn from Love and Westphal 1981).

None of the proposed mechanisms discussed thus far satisfies what could be considered three reasonable, necessary conditions for being the cause of observed cycles: (1) a significant cross-correlation between the variable and crab catch, (2) the process itself be cyclic and (3) a reasonable biological/physical explanatory mechanism. However, recent work by Johnson et al. (1986) suggests a potential mechanism that does. They have shown that spring wind stress in a southward direction is significantly correlated with crab catch typically 4 and 5 yr later (Table 1). Computed autocorrelations indicate this wind stress series is also cyclic.

TABLE 1. Estimates of correlation between crab catch from four fishing areas and spring wind stress in a southward direction (SWS) at latitudes 45°, 42°, and 39°N. Catch lags wind stress. (*) indicates significant at the 0.05 level based on the standard test.

Crab age (yr)	Lag (yr)	Washington, Northern Oregon vs SWS 45	Southern and Central Oregon vs SWS 42	Eureka, Crescent City vs SWS 42	Fort Bragg vs SBS 39
3	2.5	0.254	0.270	0.431*	0.344*
4	3.5	0.547*	0.460*	0.549*	0.402*
5	4.5	0.540*	0.531*	0.382*	0.102
6	5.5	0.244	0.537*	0.109	0.085

These correlations have a reasonable interpretation that is also testable. Since Dungeness crab larvae move into the plankton during the winter months when the northward-flowing Davidson current is strong and near the surface, it is possible that they are swept north. In some of the few studies done thus far Dungeness crab larvae have been found progressively farther offshore throughout the larval period, then near shore as megalope (Lough 1976; Reilly 1983). Thus the physical mechanism that could underly the computed statistical relationship is that successful larval settlement at each point along the coast may depend on wind-induced transport southward and/or onshore to favorable settling areas.

However, although this mechanism thus satisfies the above stated three conditions of a cyclic forcing variable, examination of the two series plotted together for a single location shows poor correspondence between them (Fig. 9). This poses a question that goes beyond the linear statistics computed thus far: could the observed wind series actually influence recruitment in such a way as to produce a catch record that is a reasonable facsimile of the observed catch record, and if it could, under what conditions would it. The answer to this question involves evaluation of the possibility that two categories of mechanisms, population dynamics and environmental forcing, are acting together.

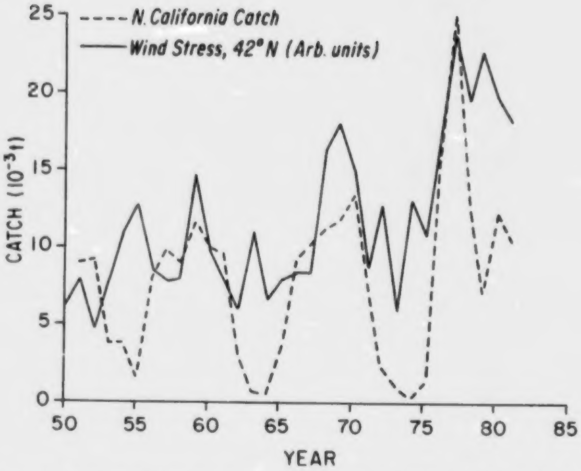

FIG. 9. A comparison of the Dungeness crab catch record from northern California with wind stress at 42° four years earlier (from Johnson et al. 1985).

Environmental Forcing with Population Dynamics

Comprehensive evaluation of the potential causes of observed cycles requires analysis of models that include both environmental forcing and population dynamics, both with and without density-dependent recruitment. This allows rejection of those combinations of population dynamics and environmental forcing mechanisms that do not lead to behavior similar to that observed.

For most populations of marine animals, year-class size is presumed to be largely determined by the effect of density or environment on the larval or early postlarval stages (Hjort 1914). The catch record that results from a population in which a fluctuating physical environment affects recruitment can be determined by applying a random input (the fluctuating environment) to models similar to those used earlier in the stability analysis. Three different types of models, corresponding to three different potential ways that the environment and the population could interact, are evaluated here.

In the first model, recruitment depends only on the environmental variable and there is no density-dependence. The only effect of "population dynamics" in this case is the fact that catch, rather than recruitment, is the observed variable. Catch is the weighted sum of past values of recruitment, in which the weighting function depends on past harvest rates and the fraction of each cohort available to the fishery at different ages.

$$\text{Catch}_t = H \sum_{i=1}^{T} \sigma_i a_i R_{t-i}$$

where σ_i = survival to age i without fishing mortality

$a_i = \sum_{j=1}^{T} p_j h_{i-j}$

p_j = fraction of age class that becomes of legal size at age a

$h_i = (1-H)^i \quad i \geq 0$

$= 0 \quad i < 0$

H = harvest rate

T = maximum age

If catch were expressed in terms of weight rather than numbers, each survival term σ_i, would be multiplied by weight at that age. See Botsford (1984) for the basis of this expression.

In the second model, recruitment into the stage susceptible to the environment is effectively constant, the environment affects that stage in a multiplicative fashion, and the result is then affected by a density-dependent mechanism. In the case of the crab this could correspond to a constant "carrying capacity" in the early larval period (that was always exceeded by total annual egg production), followed by an influence of wind on successful settlement, then a density-dependent recruitment mechanism (such as cannibalism) on post-larval stages. Recruitment in this case would be expressed as

$$(5) \quad R_t = B_e(1+v_t)f\,|C_t|$$

where B_e = assumed constant reproduction
v_t = a zero-mean random variable that represents the environment

The resulting recruitment is used in equation (4) to compute catch. This model is essentially the same as the "constant recruitment" case in Botsford and Wickham (1978), with noise added.

The third model is similar to the second except that recruitment to the stage that is susceptible to the environment is determined from total annual egg production (B_t). Recruitment in the model for this case,

$$(6) \quad R_t = B_t(1+v_t)f\,|C_t|$$

is the same as equation (1) except that environmental variability is added. Again, the resulting recruitment is used in equation (4) to compute catch.

The effect of environmental variability on the catch record will be different for each of these possible mechanisms. Only a qualitative analysis of the results of simulation of these models is given here. (A complete, mathematical description is in preparation.) Since the first model is essentially a weighted sum, its effect is to integrate and smooth the environmental time series. The resulting catch record will have fewer high frequency components and lower variability. Increases in either the number of age classes fished or the number of years required for an age class to grow into the fishery (i.e., grow to a size such that all individuals in the age class are greater than the minimum size limit) will increase the smoothing and decrease high frequencies.

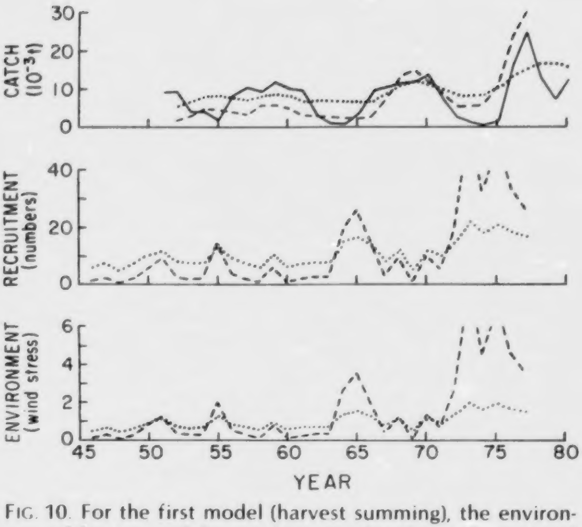

FIG. 10. For the first model (harvest summing), the environmental forcing and the resulting simulated recruitment and catch using wind stress (. . .) and wind stress cubed (- - -) for northern California. The actual catch record is shown for comparison (——).

As a particular example, results of simulating the first model with southward wind stress from 42°N as the environmental input, growth and survival parameters from the northern California Dungeness crab populations (Botsford and Wickham 1978; Botsford 1984), and a constant harvest rate of 0.6 are shown in Fig. 10. For these conditions the simulated catch record does not match the actual catch record closely. A possible cause of this disparity is that fluctuations in wind at low amplitudes have little effect on recruitment while strong winds have a much greater effect. An example of one such nonlinear effect is also shown in Fig. 10. The resulting catch record matches the actual catch record more closely except for the first peak in the 1950's.

The second model exhibits more complex behavior and requires several more assumptions regarding population dynamics. A density-dependent recruitment mechanism must be assumed which involves assuming the function c_a, the relative effect of an individual of age a on density-dependent recruitment, and a value of K, the slope of recruitment survival at equilibrium. For c_a we have used the function given earlier for cannibalism. For this model the values of K, the stability limit for K below which the population is unstable, is then approximately -1.75. The value of K used in the simulations was chosen to be -1.5, a value low enough to exhibit oscillatory behavior but not so low as to be unstable. (More negative values would lead to continuing oscillations regardless of the input).

The overall effect of this model is to attenuate frequencies both below and above the frequency at which the model would oscillate if it were unstable. The frequency response of this model depends on the function c_a and K, but can be generally characterized as becoming narrower as the population becomes less stable (Botsford and Brittnacher, unpublished ms). These "bandpass" characteristics caused by the density-dependent recruitment are smoothed by the harvest summing effect described in the first model.

As a particular example, results of using the same wind stress in this second model are shown in Fig. 11. Note that in this case, recruitment is not identical to environmental input. Again, the simulated catch record is a poor facsimile of the actual catch, both in terms of amplitude (overall amplitude of oscillations is lower) and phase (e.g., the last peak increases too soon). Making the effect of wind nonlinear again improves the correspondence considerably, however the first peak is still not present.

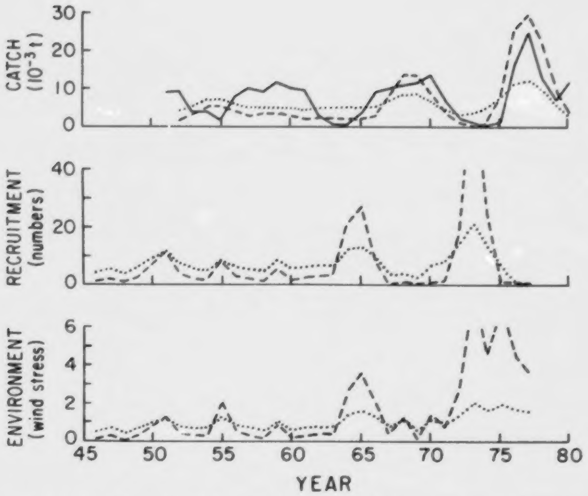

FIG. 11. For the second model (density-dependent recruitment with constant reproduction), the environmental forcing and the resulting simulated recruitment and catch using wind stress (. . .) and wind stress cubed (- - -) for northern California. The actual catch record is shown for comparison (——).

The third model requires knowledge of still more parameter values, and its behavior is slightly different. Since this model includes reproduction explicitly, fecundity, b_a, must be specified. We have used earlier published values for Dungeness crab (Botsford 1984; Botsford and Wickham 1978).

The response of this model differs from the second model in that the shape of the frequency response is changed slightly and the population is made more stable by addition of the effect of fecundity. Because of the latter, K' for this model is approximately -2.75. We have therefore used a value of $K = -2.5$. As can be seen in Fig. 12 the poor correspondence between simulated and actual catch is again improved considerably by introducing a nonlinear effect of wind. Note the presence of the initial peak in the 1950's which was not present with the other two models. For the third model, other influence functions, c_a, were also used with qualitatively similar results. For example, the results of letting c_a be proportional to fecundity (i.e., density-dependent fecundity) differed only in that the increase to the last peak began one year later and that peak was not as high.

Conclusions can be drawn from this analysis by rejecting those combinations that are qualitatively unreasonable. On this basis it appears unlikely that harvest summing of a linear effect of wind only could be causing the observed catch record. Either a nonlinear effect of wind or density-dependent recruitment or both must be involved.

The fact that a nonlinear influence of wind on recruitment is necessary presents no real problem, but rather would be expected in a transport mechanism. If successful settlement depends on wind transporting larvae to favorable areas, then with low winds no larvae would reach these areas, while with high winds many could reach these areas. It is of interest that a scenario by which larvae are swept north during the early larval period and subsequent, successful settlement depends on southward wind transport, is consistent with the increase in relative amount of variability in crab catch with distance south (see Fig. 1). Because of a similar nonlinear effect, the area furthest from the "source" would have high settlement only during highest wind years.

It should be noted that effects of a delayed response of effort to abundance were not included in simulations of combined effects of environment and population dynamics. Inclusion of estimated harvest rates from Methot and Botsford (1982) would not produce realistic results because of lack of synchrony between simulated abundance and the estimated harvest rates. The lagged effort model in Botsford et al. (1983) could, however, be included. Results would differ slightly in that the "density-dependent response" to changes in amplitude would occur at slightly greater lags.

Discussion

Evaluation of potential causal mechanisms using the available data has lead to a range of possible causes, from environmental forcing by itself to density-dependent recruitment by itself. Simulation and analytical results demonstrate that these two extremes and varying degrees of density-dependence and environmental forcing between them could produce the observed cyclic behavior. Thus it is difficult to determine from the available data which class of mechanisms is causing the cycles. This fundamental ambiguity arises from the fact that these populations cycle at a period of roughly twice the mean age of the population and there is a related environmental variable that appears cyclic at the same period. Because of this ambiguous situation, a mechanism such as the egg-predator worm can be rejected as the sole cause of cycles, but may still be involved in conjunction with a moderately cyclic environmental variable.

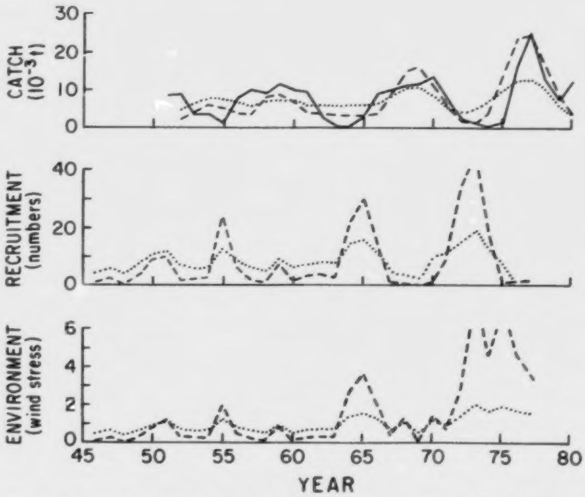

FIG. 12. For the third model (density-dependent recruitment with reproduction), the environmental forcing and the resulting simulated recruitment and catch using wind stress (. . .) and wind stress cubed (- - -) for northern California. The actual catch record is shown for comparison (——).

Even within this spectrum of possibilities, although several of the possible mechanisms match observed behavior closely enough not to be rejected, no single demonstrated mechanism completely concurs with observations. For example, the period of cycles expected from cannibalism (as currently modeled) is one or two years lower than the observed period, although this does not appear to be a problem when cannibalism acts in conjunction with environmental forcing. Other examples are the problems associated with wind-induced larval transport mechanism. Comparison of wind data with the pre-season abundance estimates of Methot and Botsford (1982) indicate that wind events do not cause the large year classes that are responsible for high abundance during the first year of each high period (Fig. 1). Also, use of a different estimate of wind stress indicates lower lag times and, for one location, lower correlations.

Fortunately, these extant problems stem merely from a lack of appropriate data of sufficient quality to resolve the issue, hence are solvable. Inferences from statistical relationships between estimates of coarse environmental variables and aggregate population variables are inherently limited to demonstrating only that one of several possible mechanisms *may* be the cause of observed phenomena. Verification (or rejection) of any of these mechanisms requires actual field measurement. The next step in analysis of the cause of these cycles, therefore, appears to be field measurement of actual larval drift, associated oceanographic and meteorological variables, and intra-population interactions following settlement. These studies are currently being planned. We are also analyzing plankton data collected over the last three years off Washington, Oregon, and California by a joint NMFS/USSR cruise. Preliminary indications from these data are that later larval stages appear to be more abundant further north (off Washington), which is consistent with the proposed northward transport by the Davidson Current.

Existing uncertainties regarding Dungeness crab population dynamics present a difficult problem for management. In setting fishery size limits and fishing effort, one is basically deciding whether to remove animals of a certain size by comparing their current market value to their "future value" (Botsford 1981a). The latter (the adjoint variable in optimal control theory) includes future growth to a larger size, then later harvest, future reproduction, and future influence on density-dependent recruitment. This implies that if density-dependent mechanisms were significant in these populations, the "future value" of individuals would be different than if density-dependent mechanisms were not dominant, and consequently optimal management policy would be different. It also implies that to set management policy, survival rates must be known. Poor knowledge of the mechanisms controlling recruitment and male survival are major sources of uncertainty in management of these populations. [See Methot (this volume) for a discussion of the management implications of uncertainty in the natural mortality rate of males.]

Although the presence of environmental variability has been acknowledged by others in theoretical analyses of fisheries, results obtained thus far do not provide a solution to the particular problem faced here. Effects of environmental "noise" on logistic-type models have been evaluated, and policies have been designed to reduce harvest variability for these types of models (May et al. 1978; Mendelssohn 1980). Others have considered the effects of random variability on stock-recruitment relationships and have designed harvest strategies that serve to increase knowledge of the stock-recruitment relationship (Walters 1981; Walters and Ludwig 1981; Ludwig and Walters 1981; Ludwig and Walters 1982). However, in determining optimal management for Dungeness crab there is uncertainty, not just in the specific form of the stock-recruitment relationship, but rather in which process controls recruitment (there may not actually be a stock-recruitment relationship of any significance). This aspect, plus the prospect of using available environmental data (rather than treating it as random noise) substantially change the nature of this problem.

A common approach to dealing with this type of uncertainty, that has also been suggested for this fishery, is to decide, on the basis of current evidence, which mechanism is most likely to control recruitment (e.g. which mechanism provides the best fit to the catch data), then design management policy as though that were a true description of population dynamics. On the average, this approach will be suboptimal. It will be optimal only if the chosen mechanism turns out to be the correct one. The alternative approach to management, which we are pursuing, is to explicitly include the existing uncertainty regarding population dynamic mechanisms in the formulation of management policy. Management policy is chosen to be that policy that optimizes the fishery over a range of possible population dynamic mechanisms.

Harvest policy can also be used to aid in determination of mechanisms involved in recruitment (Walters 1981). The fact that populations driven by environmental forcing will react differently to harvest policies than those in which density-dependent recruitment is dominant could be used to differentiate between these in the crab populations. If changes in harvest policy are made that should lead to a more stable density-dependent population, yet the population continues to cycle, this would argue for environmental forcing as the causal mechanism. As examples, removal of the lagged response of effort to population abundance or attempts to maintain population size, C_t, constant would both tend to stabilize the population and would be expected to reduce the cyclic nature of the catch record if the causal mechanism were density-dependent recruitment (Botsford et al. 1983).

Earlier observations by others of relationships between environmental variables and crab catch are consistent with the larval transport mechanism described here. For example, the association between sea surface temperature and crab catch several years later (Woelke 1971; Wild 1980) may be a reflection of the fact that higher sea surface temperatures are generally associated with a stronger Davidson current and a weaker California current (i.e., greater net northward transport) (Enfield and Allen 1980; Chelton et al. 1982; McLain and Thomas 1983).

No mechanism has been demonstrated for the sunspot relationship of Love and Westphal (1981) nor for any other relationship between sunspots and meteorological or biological phenomena. Although these processes appear to be of different period and the value to management of a demonstrated causal connection is dubious, the possibility is of some scientific interest. In light of various statistical relationships between climatic and oceanographic phenomena (e.g., Favorite and Ingraham 1976 regarding a relationship between sunspot activity and the position of the center of the Aleutian low pressure system), it is conceivable that there is a causal connection between sunspot activity and coastal currents, and therefore larval transport.

Some aspects of results presented here for cyclic populations from northern California to Washington are consistent with results obtained by others for the central California population. Winnor (1966) found significant correlations at a lag of 4 yr between central California catch and three environmental variables averaged over January through April: local shore temperature (negative correlation), sea level height (negative correlation), and southward alongshore geostrophic winds (positive correlation). Correlation at the same lag between catch and onshore geostrophic winds was not significant. He interpreted these results in terms of prevailing currents and their effect on larval drift. These correlations are consistent with southward transport being beneficial to crab larval settlement and conversely, northward transport being deleterious.

The California Department of Fish and Game has recently completed a study of the possible causes of the collapse of the central California fishery (Wild and Tasto 1983). They conclude that oceanographic changes in the late 1950s (i.e., higher temperatures, higher sea levels, stronger Davidson current) may have precipitated the decline. Mechanisms proposed are: (1) a deleterious effect of warmer water on egg survival and hatching success and (2) enhanced northward drift during the larval period because of a stronger Davidson current. Although discounted by the California Department of Fish and Game report, the possibility that the egg-predator worm caused the decline in the central California fishery is still under investigation both in the field and through analysis. Hobbs and Botsford (unpublished ms.) outline conditions under which the worm–crab system can shift between equilibrium levels.

There are several possible reasons why catch records for British Columbia and Alaska do not exhibit the same cyclic behavior of those further south. Populations off Washington, Oregon, and California are intensely fished, hence a large fraction of legal males are taken within a few months after the season begins each year. Fisheries further north are less intense and for the most part are year round. Because of these characteristics, annual landings from the more southerly fisheries might more closely reflect the strength of individual year classes than would landings from those fisheries further north. A second possible reason is the fact that these populations lie north of the point where the West Wind Drift bifurcates into the Alaska Current and the California Current. Because of this, oceanographic influences would be expected to be different. These differences may also be responsible for differences in life history between the northerly and the southerly populations.

Since mechanisms described here are similar to those described for other invertebrate species, considerations reviewed here may be relevant to invertebrate stocks in general. Wind-induced larval transport has been implicated as an important factor in recruitment of several crustacean species. For example, one hypothesis proposed for the return of larval blue crab (*Callinectes sapidus*) to Chesapeake Bay involves onshore transport of larvae in the neuston by winds during the late larval period (Johnson 1982; Johnson et al. 1984). Also, Ennis (1983) found that off the northeast coast of Newfoundland, larvae of four decapod species, *Cancer irroratus, Homarus americanus, Hyas araeneus*, and *Chionoecetes opilio*, were found near the surface and their location depended on whether winds were onshore or offshore. Three other decapod species, *Pasurus acadianus, P. arcuatus*, and *Eualus pusiolus*, were found in subsurface waters, and their location did not depend on wind direction. As another example, phyllosoma larvae of the western rock lobster (*Panulirus cygnus*) near Australia are swept offshore by winds during the early larval period (Phillips 1981).

Wind-induced larval transport is a subset of general larval transport by currents, a mechanism whose importance to recruitment was first pointed out in the classic work by Hjort (1914). This transport may be passive or larvae may actually migrate vertically through layers of currents of varying velocity, a mechanism first described by Hardy (1935). The latter type of mechanism has not been proposed for the Dungeness crab (the vertical distribution of the larval stages is not well known), but it has been implicated in larval transport of other invertebrate species, both in the open ocean and as a means of retaining larvae in or returning larvae to estuaries (Sandifer 1975). Sulkin and Epifanio (this volume) review the evidence for a mechanism for onshore transport of the blue crab (*C. sapidus*) that depends on vertical migration. Also, vertical migration and onshore transport by subsurface currents have been proposed as the mechanism that aids in the return of the western rock lobster (*P. cygnus*) to the Australian coast (Phillips 1981). Analysis and identification of the effect of mechanisms such as these on recruitment will require more complex models which include the effect of vertical migration on horizontal transport (Rothlisberg 1982; Rothlisberg et al. 1983).

In addition to the effects of wind on larval transport, other wind effects on crustacean larvae are possible. For example, wind-induced upwelling can affect larvae through increased primary production and decreased temperature (Rothlisberg and Miller 1983). Another effect of wind, the turbulent mixing of surface waters, has been proposed as a negative influence on larval fish survival because it breaks up patches of high concentrations of food (Lasker 1978). Also, proposals of wind-induced transport mechanisms should not be taken to imply that larvae are immobile drifters. Swimming abilities of the final stages of some crustacean larval species have been suggested as a mechanism aiding in return to favorable setting areas [e.g., the puerulus stage in *P. cygnus* (Phillips 1981)], and the swimming ability of the megalopal stage of *C. magister* may also contribute to successful larval settlement.

The combined role of density-dependence and environmental forcing on recruitment has been suggested for other invertebrate populations. For example, the eventual effect on year class size of any variability in settlement of the western rock lobster (*P. cygnus*) was thought to be minimal because settlement always exceeds the "carrying capacity" (determined by food and shelter) of the nursery reefs (Chittleborough and Phillips 1979). Research since then has led to a better definition of when density-dependent recruitment occurs (Morgan et al. 1982) and the potential effects of oceanographic conditions on recruitment (Phillips 1981). As another example, Caddy (1979) in his investigation of the cyclic Bay of Fundy scallop fishery, examined the possibilities that density-dependent recruitment, environmental forcing, or a combination of these was responsible for cycles.

It should be noted that multiple regression approaches to combinations of environmental and density-dependent mechanisms may not be effective for cyclic populations such as the Dungeness crab. Nelson et al. 1977, Parrish and MacCall 1978 and others have analyzed variability in fish populations by fitting both a stock-recruitment curve and environmental variables in the same model. However, for cyclic populations in which the period of cycles is approximately twice the reproductive age, a stock-recruitment relationship constructed from the catch data would merely reflect the cyclic nature of the catch record. Since the cyclic nature of the catch record may be caused by the environment, removing it before testing for covariation with an environmental variable could prejudice the procedure against finding a relationship when one actually existed.

Although computed correlations between environmental variables and recruitment or stock and recruitment do not constitute proof of the existence of a mechanism governing recruitment (but should be verified by field studies) two other caveats regarding their use in these kinds of studies may be useful. The first is that a computed correlation coefficient does not depend on relative amplitudes and coefficients of variation of the two series. It can be viewed as an "amplitude free" measure of the mean squared error between the two series. Because of this a time series with a coefficient of variation of only 0.1 may be highly correlated with a time series with a coefficient of variation of 0.5, whereas any causal link between them would require a nonlinear mechanism.

The second caveat regards the statistical significance of correlation coefficients computed from time series. Standard results regarding sampling distribution of correlation coefficients do not apply because they assume that samples in each series are independent. Fisheries and environmental time series are likely to have some intra-series dependence. Evaluation of the significance of these correlation coefficients, therefore, requires that intra-series correlation be taken into account. The most common approach to this problem is to attempt to estimate the variance of the estimate of correlation in a way that includes the effect of intra-series correlation. Box and Jenkins (1976) recommend use of Bartlett's (1946, 1966) expressions. Botsford and Wainwright (unpublished ms.) have developed an alternate expression that does not depend on large sample sizes. Chelton (1983) provides further discussion and a regression-oriented approach to this problem.

In summary, although the dynamics of cyclic Dungeness crab populations is not completely understood, the use of available data, modeling results, and computed statistical relationships has narrowed the field of possible causal mechanisms underlying cycles in these Dungeness crab populations. Two proposed predator-prey mechanisms have been discounted, but density-dependent recruitment, environmental forcing, and a combination of these remain as possibilities. The former category includes cannibalism, density-dependent fecundity or some form of density-dependent larval survival as possibilities. Possible mechanisms in the environmental forcing category include wind or other phenomena that could affect larval transport. Possible combinations of density-dependent and environmental mechanisms would include an influence of wind on larval transport and successful settlement followed by cannibalism by adults, or density-dependent reproduction followed by an influence of wind on the fraction of larvae that successfully settles. Determination of which of these is the cause of cycles will depend on direct field measurements of potential mechanisms. Studies such as these appear to be important to management. Since the combination of physical and biological mechanisms encountered in these studies have much in common with those other invertebrate (and fish) species, problems encountered will be similar and there is some benefit in exploiting these commonalities.

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Production and Exploitation of the Crayfish, *Orconectes virilis*, in Northern Climates

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The temperature regime at northern latitudes sufficiently controls cohort growth rates of Cambarid crayfish so as to confine production within a very narrow range of values, regardless of whether stocks are exploited. Production in these high nutrient study lakes (Dock and Shallow lakes, Ontario) was actually lower than in previously studied low nutrient lakes. This is because the lower growth rate in low nutrient lakes is somewhat compensated by higher survival rates of juveniles resulting in higher biomass production. At these northern latitudes, low temperatures inhibit juvenile growth. As a result, the maturity molt of an individual is induced at a relatively small size, even in nutrient rich habitats. Once the maturity molt occurs, frequency of molting is greatly reduced. Because of this, growth compensation in adults is not possible even when densities are reduced by 50%. The absence of dramatic density dependent compensation in growth combined with a limited fecundity response inhibits the detection of growth overfishing in crayfish populations at northern latitudes. As a result, populations could be easily exploited to the recruitment overfishing stage. Such populations, subjected to a succession of years exhibiting poor climatic conditions for optimum cohort recruitment, could undergo sudden unpredictable stock reductions, resulting in wide oscillations in production and yield. At lower latitudes, the greater potential for rapid juvenile growth makes overrecruitment and stunting a far greater threat to limiting production than overfishing.

Aux latitudes septentrionales, le régime de température contrôle suffisamment les taux de croissance des cohortes d'écrevisses de la famille des Cambaridés pour limiter la production à un très étroit écart de valeurs sans tenir compte de l'exploitation des stocks. Dans les lacs expérimentaux Dock et Shallow (Ontario) à teneur élevée en bioéléments, la production était en réalité inférieure à celle observée auparavant dans des lacs à faible teneur en bioéléments où le plus faible taux de croissance est quelque peu compensé par des taux de survie plus élevés des juvéniles, ce qui entraîne une production de biomasse améliorée. Aux latitudes septentrionales, les basses températures inhibent la croissance des juvéniles. La mue de maturité d'un individu est donc provoquée à une taille relativement peu élevée même dans les habitats riches en bioéléments. Une fois cette mue effectuée, la fréquence des mues diminue considérablement. Ainsi, les adultes ne peuvent pas grossir même quand les densités sont réduites de 50 %. L'absence d'une compensation remarquable de la croissance liée à la densité combinée à une fécondité limitée ne permet pas de révéler une surexploitation des populations d'écrevisse aux latitudes septentrionales. Les populations pourraient donc être facilement exploitées jusqu'au stade de surpêche de la population vulnérable. De telles populations soumises à plusieurs années consécutives de conditions climatiques nuisibles au recrutement optimum de cohortes pourraient subir des baisses imprévisibles soudaines du stock entraînant de grandes fluctuations de la production et du rendement. Aux plus basses latitudes, le potentiel plus élevé d'une croissance rapide des juvéniles fait de la surexploitation et de l'arrêt de la croissance de plus grandes menaces pour la limitation de la production que la surexploitation.

Crayfish have long been economically important to Europeans (Brinck 1975). In North America, wild crayfish stocks are intensively exploited only in California (McGriff 1983) and Louisiana (Comeaux 1975). As these crustaceans gain culinary acceptance in North America, fisheries for them may become widespread. Many Canadian boreal lakes, being limnologically similar to those in Scandinavia, could support crayfish fisheries.

Despite their long historical use in Europe, little is known about the management of wild crayfish populations. This study attempts to observe and measure the qualitative and quantitative response of crayfish stocks to experimental exploitation in two northern Ontario lakes in order to devise an appropriate management regime for crayfish stocks applicable to northern climates.

The first question that comes to mind is can crayfish stocks be overexploited? Secondly, can we detect the process of overfishing? If overfishing occurs will the response of crayfish populations be similar to that of finfish? Will management models or schemes implemented for freshwater fin fish populations be applicable to freshwater crayfish? Or shall we have to devise an alternate or modified management regime?

This problem was first addressed in a 10-year study of *Orconectes virilis* inhabiting two oligotrophic Michigan lakes (Momot and Gowing 1977a,b,c). Because of secular changes in system productivity, behavioral dominance of males, and lack of a measurable growth response attributed to the nutrient poor condition of the habitat, the inferences concerning the effects of exploitation from this before-after approach were somewhat inconclusive (Momot and Gowing 1983).

In this study I made two changes in my approach. Firstly I chose a nutrient rich lake reasoning that a growth response could be easily documented as stock density was reduced. Secondly, to avoid a study involving a pre- and postexploitation period, I decided to compare two lakes simultaneously, one in which we would attempt to overexploit the population (Dock Lake) while monitoring an unexploited population in a second nearby lake (Shallow Lake). Fortunately, females were confined to shallow waters in both lakes throughout the summer. This made both sexes vulnerable to the gear employed for harvest, avoiding the complications in catch composition caused by male dominance in the previous study (Momot and Gowing 1977a,b,c).

I compared and measured yield, growth, age composition, survival, fecundity, recruitment, and production on both an annual (1976–84) and cohort (six full generations) basis. Comparisons with the previous Michigan data helped to formulate generalizations for designing a management scheme for exploiting crayfish.

Study Area

Dock and Shallow are small marl lakes located within the city limits of the City of Thunder Bay, Ontario, 19.5 km west of Lake Superior. Dock Lake is 1.2 ha, with a mean depth of 2.4 m and a maximum of 4.5 m; while Dock Lake stratifies thermally during summer, nearby Shallow remains homothermous. Shallow Lake is 1.6 ha with a mean depth of 2.2 m and a maximum of 2.4 m. Both lakes are in an early senescent stage of eutrophy, having high values for nutrients, dissolved solids, conductivity, and alkalinity (Momot 1978). The lakes have a sandy shoal area in the first 2 m overlain with soft silty substrates. Beds of the emergent sedge, *Carex aquatilis* var. *substricta*, which serve as crayfish nursery areas in small lakes lacking a rubble–cobble substrate, cover 37% of the shoreline in Dock Lake and 28% of the shoreline in Shallow Lake. *Typha latifolia* predominates the emergent vegetation of both lakes especially on the remainder of the shoreline, which is excessively silted. The lakes are located on private property, closed to public use. The study was conducted from May 1976 to September 1984.

Methods

Adult and yearling crayfish were collected with wire traps baited with fish. Young-of-the-year were sampled with hand nets. Crayfish production was estimated by the Ricker (1975) method. We carried out sequential Schumacher–Eschemeyer mark and recapture population estimates for each sex, using different marks in each year separately recorded for each sex. The accuracy, limitation, validity, and details of this technique in small lakes and ponds are described in Momot and Gowing (1977a,b,c), Malley and Reynolds (1979), Momot (1978), and Momot and Gowing (1983). These papers detail the techniques for measuring age composition, growth rate, and fecundity estimates used in calculating recruitment rates. Age composition was analyzed from size–frequency polygons and verified by following the annual modal progression of recaptured known age animals marked with a distinctive clip in each of the previous years. Growth rate was determined from a sequential series of size–frequency graphs based on the current year's catch, and verified by comparison with graphs of recaptures from individual cohorts. Fecundity was measured as pleopodal egg counts. Crayfish were harvested solely in Dock Lake with baited minnow traps whose funnel openings were enlarged to 100 mm diameter. I initially used 30 traps during a 5-day period for a total effort of 150 trap days. These initial harvest data were used in the Ricker (1975) equilibrium yield model to establish guidelines for the subsequent harvests. As a result, harvest effort increased ninefold to 1350 trap days in 1978 and increased further in 1979 to 2600 trap days (200 traps × 13 days), a level equivalent to a 17-fold increase over the initial period (1977) and nearly a twofold increase over the previous year. Harvest was continued at this rate until 1982 when harvest was further increased to 4000 trap days (200 traps × 20 days).

Results

GROWTH

With the exception of the age 0.5–1.5 interval, no consistent annual trend or pattern was evident for either the exploited or unexploited population (Fig. 1). Although the instantaneous rates of growth at age 0.5–1.5 have increased since 1976–77 in exploited Dock Lake, they also simultaneously increased in unfished Shallow Lake (Fig. 1). One noticeable event is the exceptionally good growth in both lakes of age 0 animals in 1976–77 and the poor growth of age 0.5–1.5 crayfish in the same years (Fig. 1). Although maximum size and age attained by Ontario crayfish compare with the Michigan populations (Momot 1978), the mean size at a given age is slightly higher due to the faster growth rate.

FECUNDITY

Fish populations frequently respond to exploitation through an increase in mean ovarian egg production. No such increase is apparent in the pleopodal egg production in crayfish populations of the low or high nutrient lakes (Fig. 2). Although annual values fluctuated in both the high and low nutrient lakes, the mean annual fecundity of the population of the unfished high nutrient lake (Shallow) was not significantly different than in the exploited population (Dock Lake) except for 1981 (ANOVA $F = 10.971$, $P < 0.01$, df (1,97) (Fig. 2). Note, however, that mean annual fecundity in the unfished lake was significantly lower in 7 of 8 cases (Binomial probability is 0.035). Overall the fecundity per female in the nutrient rich Ontario lakes (Fig. 2) ranged from 86 to 203 eggs per female.

ANNUAL PRODUCTION, MEAN BIOMASS AND P/$\bar{B}$ RATIOS

Annual production values were both lower and less variable than in the Michigan lakes (Momot and Gowing 1977c). The mean annual production ± SD in Dock Lake

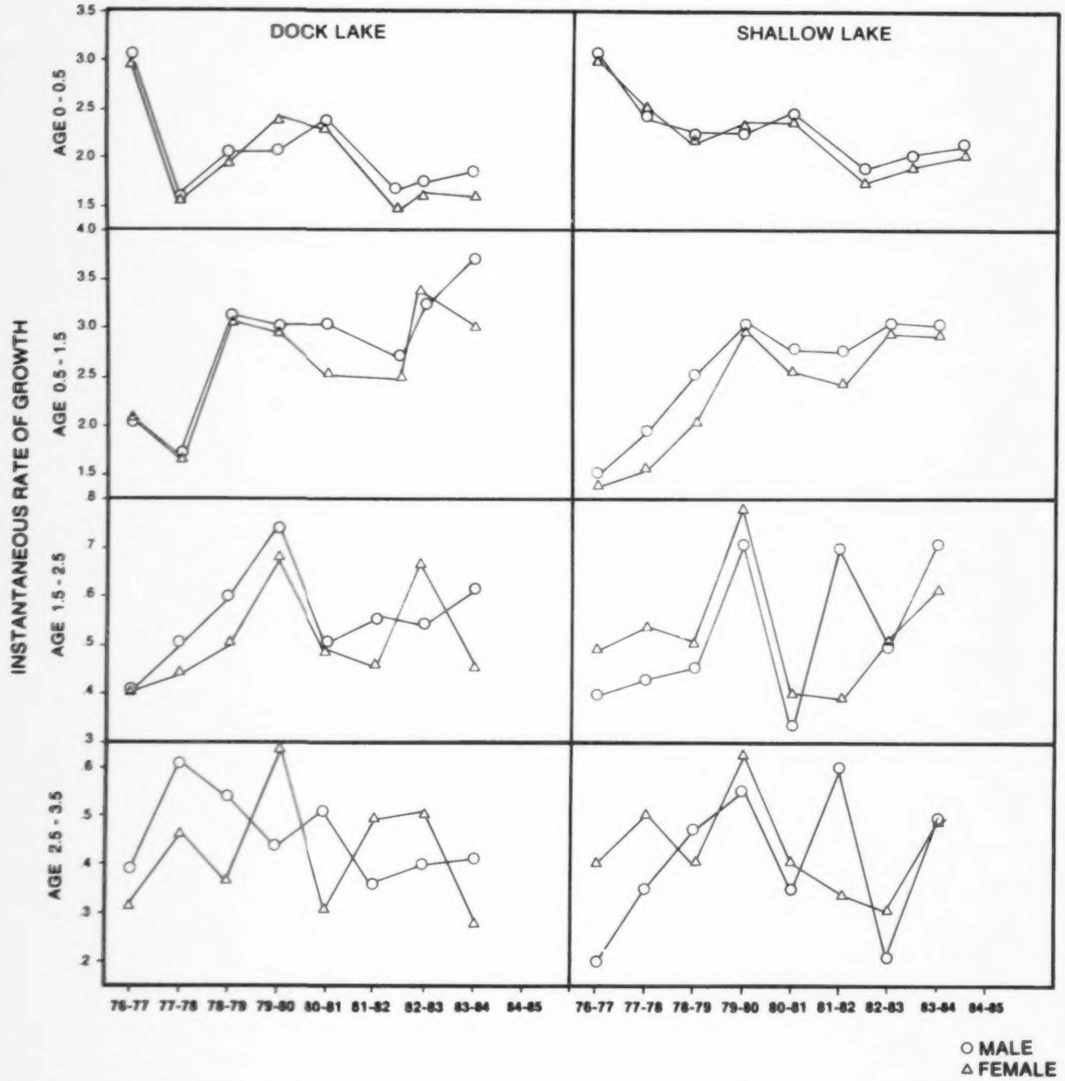

FIG. 1 Annual comparison of instantaneous rates of growth (G) during four age intervals in Dock and Shallow Lake.

was 47.5 ± 16.4 kg/ha compared with Shallow Lake where the mean annual production ± SD was 36.2 ± 7.5 kg/ha, and was significantly greater in Dock Lake ($P > 0.01$ df $= 14$, $t = 3.67$). On the whole the variance in annual production values for the Ontario lakes was twofold in magnitude. Similar trends can be noted for the mean biomass values while $P/\bar{B}$ ratios ranged in these Ontario lakes (0.8–1.9) (Fig. 3). At first, annual production decreased in the exploited population but the same trend was noted in the unexploited population (Fig. 3). More recently, production has increased in Dock Lake (Fig. 3).

AGE COMPOSITION OF THE CATCH

Because low dissolved oxygen confines females to shallow water in Dock Lake, they are much more vulnerable and constitute as much as 50% of the harvest (Fig. 4). Size and sex-related biases in trap catches serve to overrepresent males and large animals of both sexes in the catch relative to their actual density in the population. The catch per unit of effort (CPUE) data thus are of little worth as an index of relative age structure but might serve as an index of biomass in certain waters lacking serious fish predators (Fig. 5). Certain species of fish can, however, alter the behavior of crayfish making them less susceptible to trapping (Collins et.al. 1983; Capelli 1975; France 1983).

ANNUAL YIELD

At a low effort (150 trap days) males at first dominate the catch, but as fishing pressure increased the proportion of females rose (Fig. 4) so that following 1979, we harvested between 36 and 77% of males and between 30 and 51% of the females estimated to be

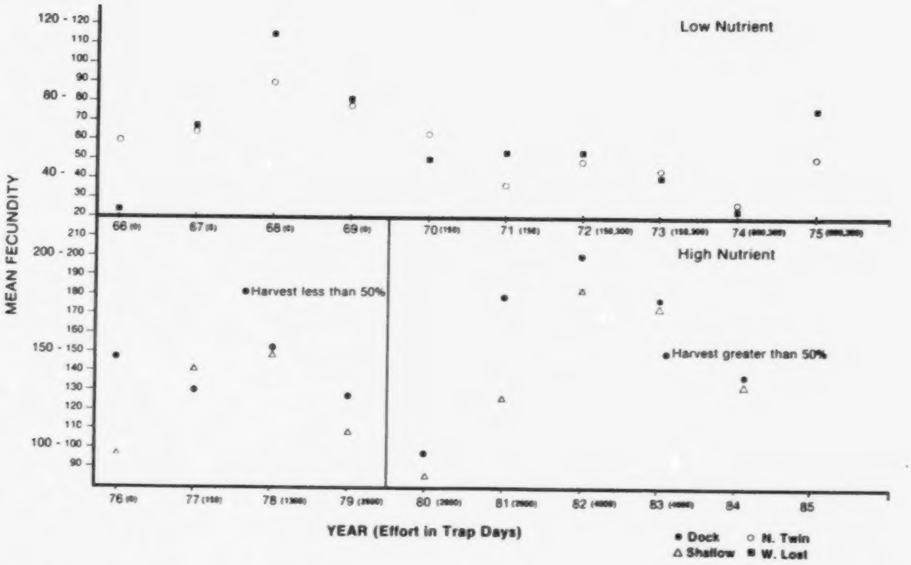

FIG. 2. Comparison of mean fecundity of crayfish measured in two lake sets consisting of low nutrient West Lost and North Twin Lake, Michigan, and Dock and Shallow Lake, Ontario and compared to annual effort in trap days. (In the upper figure the first number where two numbers are given refer to West Lost, the second to North Twin). The high nutrient data is divided into two periods 1976–79 when the harvest rate of the exploited stock (Dock Lake) was less than 50% and 1980–83 when it exceeded 50%.

vulnerable to the gear (Fig. 4). In 1978, when effort was increased to 1350 trap days, yields correspondingly increased to 12.0 kg/ha. Somewhat surprisingly, an increased effort of 2600 trap days from 1979 to 1981 produced somewhat lower yield: 7.3 kg/ha in 1979, 10.5 kg/ha in 1980, and 9.0 kg/ha in 1981 (Fig. 4). These lower yields reflect lower densities and availability of catchable-sized crayfish in the lakes during that period. When effort increased to 4000 trap days in 1982, 1983, and 1984, the yield increased to 22.8 kg/ha in 1982, 30.9 kg/ha in 1983, and 27.0 kg/ha in 1984. Reflecting both the increased density of catchable-sized crayfish as well as the greater effort expended (Fig. 4).

Catch per unit of effort, expressed as kilograms per trap day (TD) per hectare, was an order of magnitude higher in Michigan than in the high nutrient Ontario lakes. It ranged from 0.008 to 0.166 $\mathrm{kg{\cdot}TD^{-1}ha^{-1}}$ in the low nutrient lakes compared to 0.003 to 0.014 $\mathrm{kg{\cdot}TD^{-1}ha^{-1}}$ in the high nutrient lakes (Fig. 5). Summer biomass in kilogram per hectare was significantly correlated with the CPUE expressed as $\mathrm{kg{\cdot}TD^{-1}ha^{-1}}$ only in West Lost Lake ($r = 0.96$), for North Twin $r = 0.09$, and Dock Lake $r = 0.17$.

COHORT PRODUCTION AND YIELD

Although yields from a fishery are usually recorded on an annual basis, a far greater insight into the dynamics of the response of a population to fishing is obtained by examining the response of individual cohorts (year-classes) to exploitation.

To facilitate the study, each cohort's life cycle was divided into four periods: age 0–0.5, 0.5–1.5, 1.5–2.5, 2.5–3.5 years of which the last three age intervals are susceptible to harvest. Three consecutive cohorts (1976, 1977, 1978) were subjected to progressively increased levels of exploitation — 150, 1350, and 2600 trap days — while portions of the 1979, 1980 and all of the 1981 cohorts have been exploited at rates increasing from 2600 to 4000 trap days per season. The first susceptible age group of the moderately fished 1977 cohort was subjected to a transitional rate of 1350 trap days while the last two age groups were harvested at a rate of 2600 trap days. Since 1978, all cohorts have been subjected to a minimum effort of 2600 trap days and certain age groups (age III — 1979 cohort, ages II and III — 1980 cohort, all of the 1981 and 1982 cohort) to 4000 trap days. Yields during this fishing-up process have ranged from 7.5 to 29.3 kg while cohort production has ranged from 35.3 to 75.9 kg (Table 1), approximately a twofold variation. With each succeeding year, a larger proportion of each cohort's production has been diverted into yield as evidenced by the evident decrease in the PC/YC ratio (Table 1). The trend signifying a decrease in production since 1978 cannot be attributed to the fishing-up process since a similar decline is also evident in the unfished population of Shallow Lake (Table 1) and production increased in 1984 in Dock Lake despite the high removal.

In contrast to what often occurs in finfish fisheries during a fishing-up process, both production and yield of the crayfish population have remained relatively stable. This stability is displayed by crayfish populations because large cohorts normally suffer higher mortality rates than small cohorts (Fig. 6) with the result that populations are well regulated. The same seems true of the populations in the Michigan lakes (Momot and Gowing 1983).

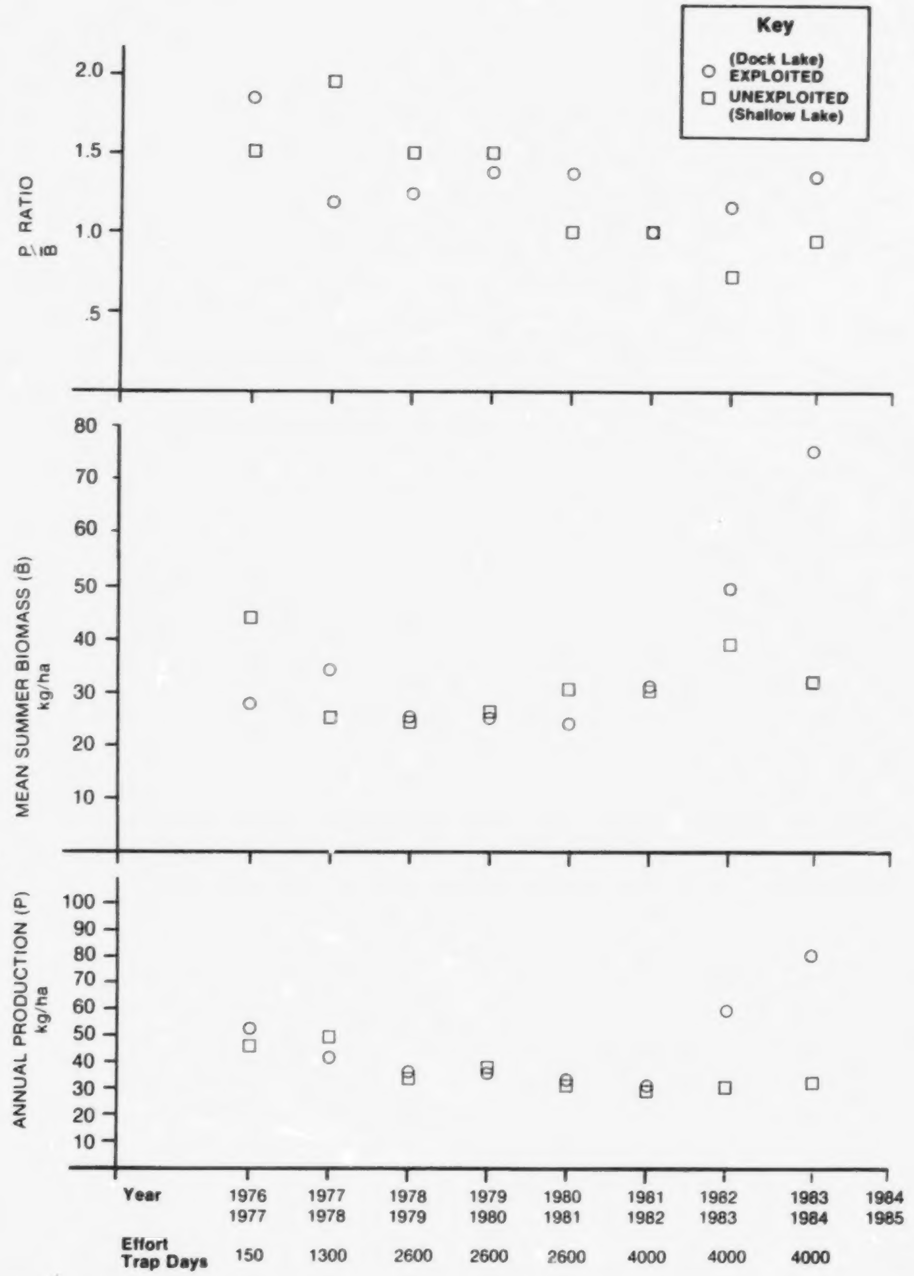

FIG. 3. Comparison of annual production, mean biomass and P/B̄ ratio between the exploited population of Dock Lake with the unexploited stock of Shallow Lake.

Density dependent survival is well established during the first growing season (Fig. 7) with quality and size of nursery area affecting first year survival. Dock Lake has a nursery area of the same size as Shallow Lake (2328 m^2 vs. 2243 m^2). Yet the first year survival is clearly greater in Dock Lake for cohorts ranging between approximately 100 and 300 thousand hatchlings (Fig. 7). The exception is the years 1976 and 1977 in Shallow Lake when hatchling densities were 60 thousand or less. At these reduced densities survival rates were much higher. The higher survival in Dock Lake for cohorts of approximately the same size is attributed to the *Carex* bed in that lake being denser (5.3 vs. 1.8 clumps/m^2), wider (1.45 vs. 0.43 m) and located over firmer substrates (50% vs. 10% clean sand). The availability of firm substrates is essential for good crayfish survival (Devcich 1979; Morrissy 1980; Momot 1977a).

Nursery habitat availability remains of far greater importance to first year survival of a given cohort than the fecundity or size of the parental stock or the number of hatchlings per m^2 (Table 2). The same seemed true of the Michigan populations (Momot and Gowing

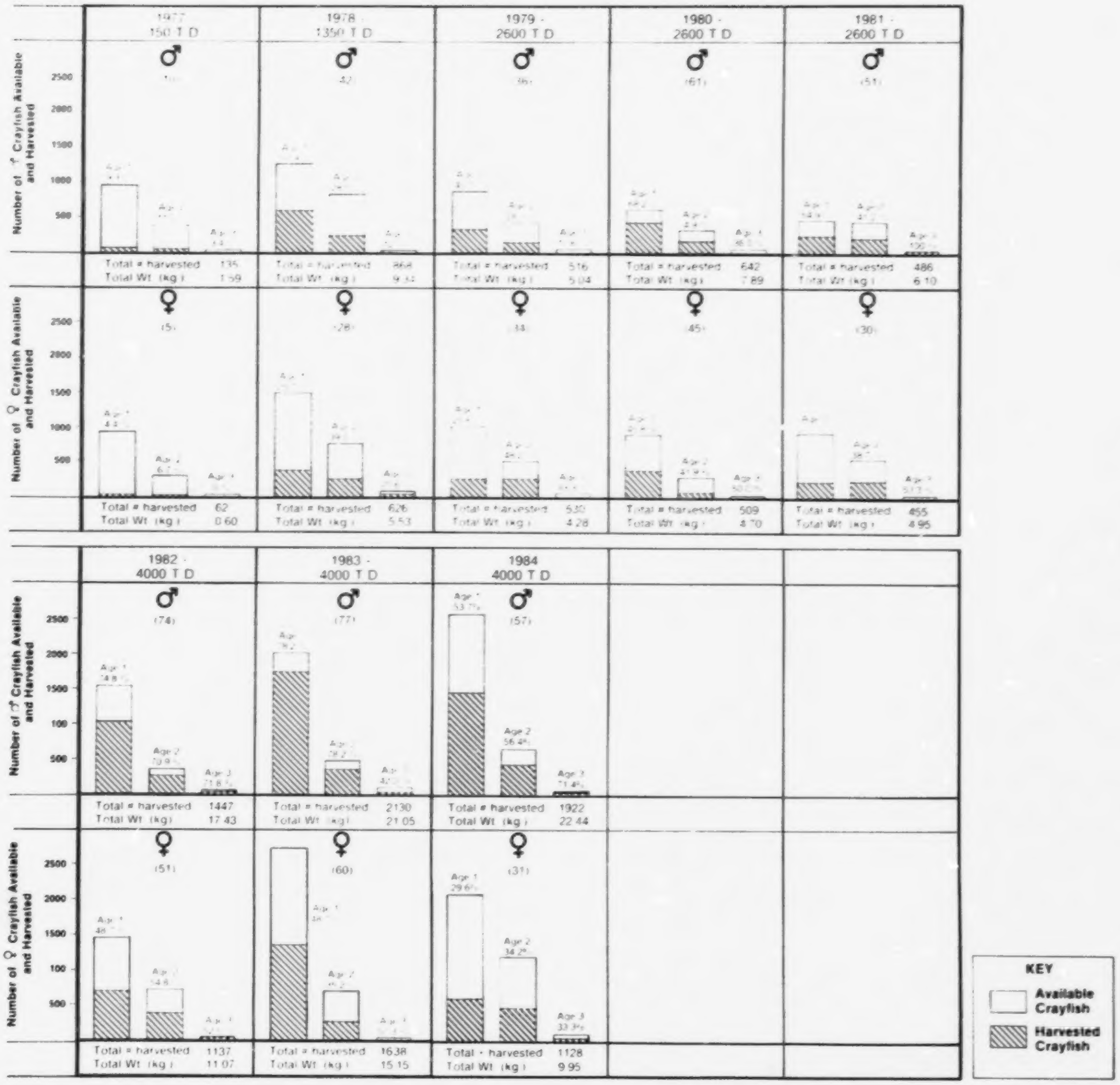

FIG. 4. Percentage of females and males comprising the total catch and catch per age group of crayfish in Dock Lake, Ontario, in relation to the annual effort expended in trap days. Data are presented as the total number and weight harvested.

1977c). Even large cohorts are reduced to less than 2% of the initial size of the brood by age 2 and when survivors are plotted as a proportion of final brood size, the proportions for large cohorts (78 and 79 in Dock Lake and 78 in Shallow Lake) are seen to fall below that of smaller cohorts (77 and 80 in Dock Lake and 77 and 76 in Shallow Lake (Fig. 6). The result of this differential survivorship is that production and biomass values fall within a relatively narrow range of values (Fig. 3).

Discussion

In northern latitudes, temperature is as important as nutrients, per se, in regulating growth. Since crayfish molt most frequently as juveniles, any factor reducing juvenile molting frequency also reduces growth rate. This in turn determines the size at maturity. For a given cohort the size at which the molt to maturity takes place is very flexible and can reflect environmental conditions (Huner 1978). Most of the opportunity for rapid growth during the life cycle of an individual crayfish must take place during the juvenile growth period prior to the maturity molt. In northern climates, the temperature of the water in the shallows, especially nursery areas, is an important determinant of the molting rate in juveniles.

High density populations in suboptimal environments suffer low molting rates, and in low nutrient lakes a reduced increment per molt; as a consequence they mature at a much smaller than normal size (Svardson 1948; Huner 1978; France 1983). While mature, stunted fish may resume rapid growth if favorable conditions reappear, crayfish, because of their determinate growth following the maturity molt, do not exhibit such abil-

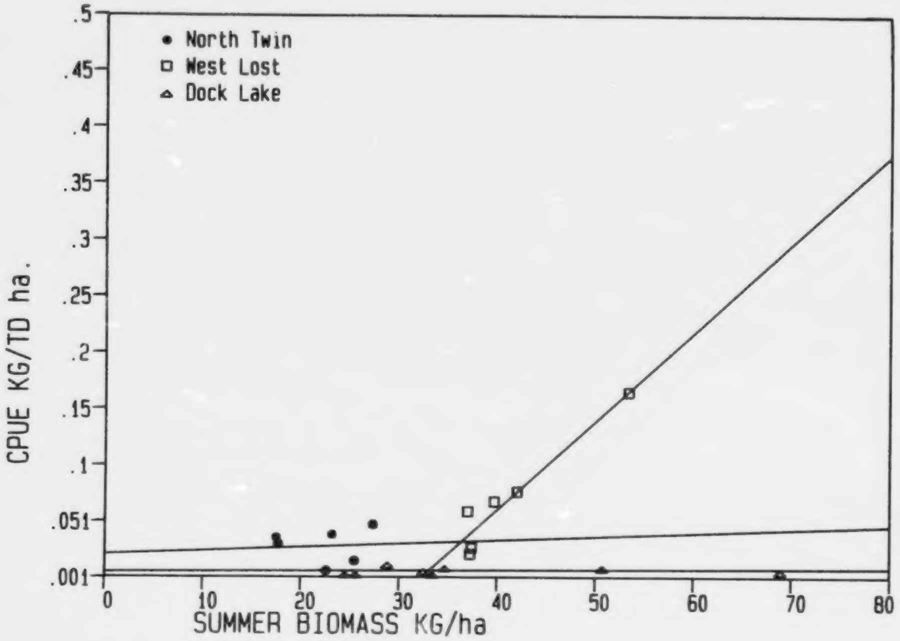

FIG. 5 Catch per unit of effort in kg per trap day compared to summer biomass in kg/ha of crayfish in three lakes.

TABLE 1. Cohort production (*Pc*), cohort mean biomass ($\bar{B}$), cohort (*Pc*/$\bar{B}$), ratios and yield (*Yc*) of six generations of crayfish in two high nutrient northwestern Ontario lakes, Dock Lake (DL) and Shallow Lake (SL). All estimates given as kg per cohort.

Cohort	*Pc*		$\bar{B}$		*Pc*/$\bar{B}$		*Y*	*Pc*/*Yc*
	DL[a]	SL[b]	DL	SL	DL	SL	DL	DL
1976-79	75.9	90.0	12.8	13.6	5.9	6.6	7.5	10.1
1977-80	67.0	82.2	11.7	13.3	5.7	6.2	13.0	5.1
1978-81	43.1	79.7	6.7	10.9	6.4	7.3	9.3	4.6
1979-82	54.2	56.4	9.0	14.2	6.0	4.0	14.3	3.8
1980-83	35.3	56.9	8.9	18.9	3.9	3.0	15.7	2.3
1981-84	48.4	46.2	13.9	12.0	3.5	3.8	29.3	1.7
1982-85[c]	75.1	57.6	25.5	20.8	2.9	2.8	36.5	2.1

[a] Exploited.
[b] Unexploited.
[c] Measurement of production and mean biomass of this cohort includes only first 3 age groups however the last age group contributes only a small fraction of the production, biomass, and yield.

ity for growth compensation, even if they are supplementally fed in thermally optimal habitats (Romaire 1976). This adjustment in size at maturity to the available food supply must be a major mechanism ensuring reproductive success of a species with a relatively short life cycle, that encounters seasonal variations in environmental conditions. At lower, warmer latitudes, e.g. Louisiana, limiting threshold levels of both food and temperature are often exceeded. As a result, a large population of crayfish grow rapidly, reaching their maximum physiological size (Momot and Romaire 1983). At higher latitudes, e.g. Northern Ontario, even if food supplies remain above a certain threshold level, low summer temperatures can drastically reduce the molting rate of juveniles. Size at maturity of Cambarid crayfish, at these latitudes, reflects *both* food supply and the thermal regime.

In the low nutrient Michigan Lakes, the poor growth

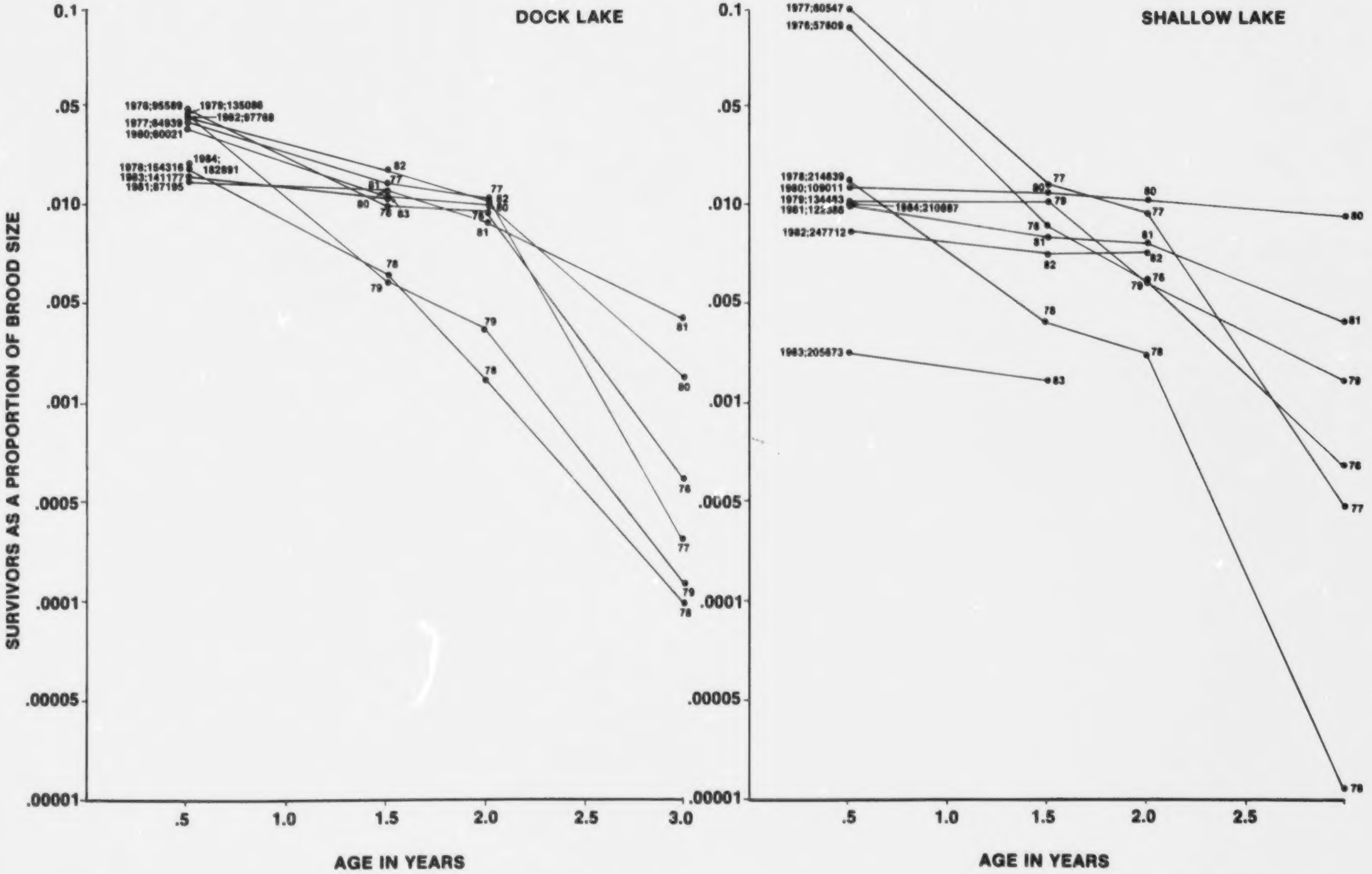

FIG. 6. Survivors at a given age plotted as a proportion of the final brood size of crayfish of different initial densities (No.). Values for initial densities are given below or alongside each year.

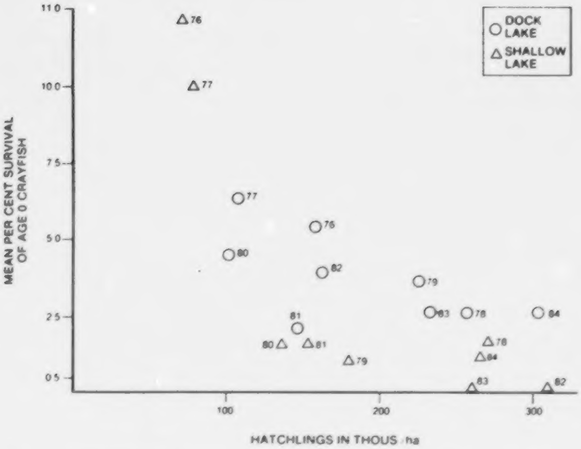

FIG. 7. Percentage mean survival of young-of-the-year crayfish as a function of density at hatching in two lakes.

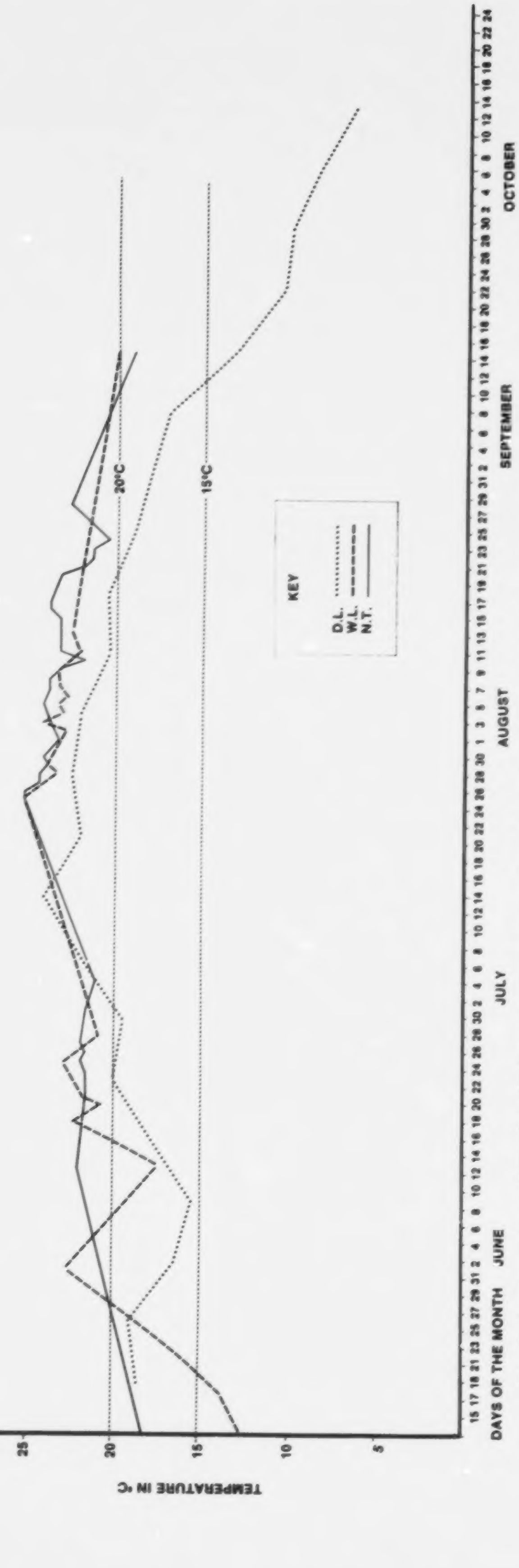

FIG. 8. A comparison of Dock Lake littoral zone temperatures in °C. for 1980 compared to West Lost and North Twin temperatures for 1966.

response may have been the result of an overcrowded population competing for scarce resources under a restrictive thermal regime. For example, when we removed between 34 and 58% of the Age II+ males, this allowed the female population to increase in population size (Momot and Gowing 1977c).

In Dock Lake, nutrient availability was high and so food was not limiting. The lack of a growth response after the removal of 36–77% of age I+ males and 30–60% of age II+ females may have been related to the lack of competition for food resources. However, when the thermal regime of Dock Lake is compared to West Lost Lake and North Twin relative to the 15°C thermal barrier, the growing season is obviously longer in West Lost (Fig. 8). Since molting is inhibited in *Orconectes virilis* at temperatures below 15°C (Aiken 1969), a rapid juvenile growth response may be precluded by the shorter growing season induced by the lower thermal stability of the shallower lake (Fig. 8). This results in a maturity molt at a reduced size and effectively prevents dramatic growth compensation even when 50% of adults are removed.

The shorter growing season and lower temperatures probably affect a fecundity response as well. If total seasonal food intake is restricted by low temperature, excess nutrient availability from a reduction in population density might not be efficiently translated into higher egg production rates per female. In the high nutrient Ontario lakes, overall mean fecundity rates were two- to threefold higher and less variable than in the low nutrient Michigan lakes (Fig. 2) suggesting that a higher nutrient supply during a restricted growing season is reflected in egg production (Fig. 2). However, a reduction in population density failed, at least over the short term, to evoke any sustained response in mean fecundity suggesting that above a certain food availability threshold, seasonal limits on food intake probably restrict the process by which excess food can be bioenergetically translated into egg production (Jones and Momot 1983). In the low nutrient Michigan lakes, food availability was so low, relative to population density, that mean fecundity was not only far below that

TABLE 2. Recruitment of crayfish in two northwestern Ontario lakes.

Year	No. eggs per m² [a]	No. young[b] per m²	No. young per adult♀	Mean percentage of hatchlings surviving to end of 1st year	Female breeding population/ha[c]
	Dock Lake (exploited)				
1976	30.38	1.64	8.01	5.4	1075
1977	20.64	1.13	7.15	5.5	830
1978	49.05	1.26	3.89	2.6	1707
1979	42.93	1.58	4.71	3.7	1765
1980	19.07	0.82	4.23	4.3	1013
1981	27.71	0.58	3.76	2.1	811
1982	31.07	1.20	7.86	3.9	801
1983	44.88	1.19	4.63	2.6	1349
1984	58.13	1.55	4.66	2.6	2092
	Shallow Lake (unexploited)				
1976	14.23	1.56	10.83	11.0	728
1977	14.96	1.51	14.24	10.0	536
1978	53.03	1.16	3.26	2.2	1802
1979	35.45	0.47	1.50	1.3	1570
1980	27.06	0.44	1.40	1.6	1592
1981	30.24	0.12	0.53	1.5	1191
1982	61.06	0.57	1.71	0.1	1683
1983	50.82	0.16	0.31	0.3	1521
1984	52.10	0.58	2.45	1.1	1914

[a] Littoral zone < 1.5 m.

[b] Number of young at the end of the first growing season generated as the total number of age 0 crayfish divided by area of the littoral zone.

[c] Defined as numbers of breeding females in the spring, divided by the area of the lake in ha.

in the high nutrient lakes (Fig. 2) but did show a response to reduction in mean density of the population (Momot and Gowing 1977a).

A third possible response to a reduction in population density is an adjustment in the age specific survival rate (Table 3). At first the more intensively fished 1978 and 1979 cohorts displayed a lower survival rate when compared to the less intensively fished 1976 and 1977 cohorts; however, this was not so for the 1980 or 1981 cohort. Although the overall replacement rate (R_o) initially fell below 1.0 (1978 and 1979 cohorts), it then increased to 2.5 for the 1980 cohort and 2.3 for the 1981 cohort. In addition, the unfished cohorts in nearby Shallow Lake manifest a similar response (Table 3). Adjustments in age specific survival within cohorts of the exploited population cannot be attributed to fishing.

We measured the success each brood had in replacing its initial number during its reproductive span in the population by integrating the survival patterns shown in Fig. 6 with the reproductive span of the population (Table 3). The cumulative replacement of the initial brood size used as the ordinate in Fig. 9 corresponds to a summation of $N_x m_x$ statistics of Table 3 divided by N_o, the initial brood size. The results seem unequivocal: regardless of whether or not the population is exploited, most of the larger broods do not manage to replace themselves, while small broods do. We can only conclude that the factors regulating population size operated either independently or concurrently with the impact of exploitation in the exploited lake. The reduced survivorship and recruitment realized in the population of the unfished lake succinctly points out the difficulty of separating or identifying the effects of fishing from other sources of mortality acting upon the population.

This study also suggests that conditions promoting a rapid juvenile growth rate rather than adjustments in egg production per se modify any stock recruitment interaction. For example, note for both lakes that the higher survival during 1976 and 1977 (Table 2) of age

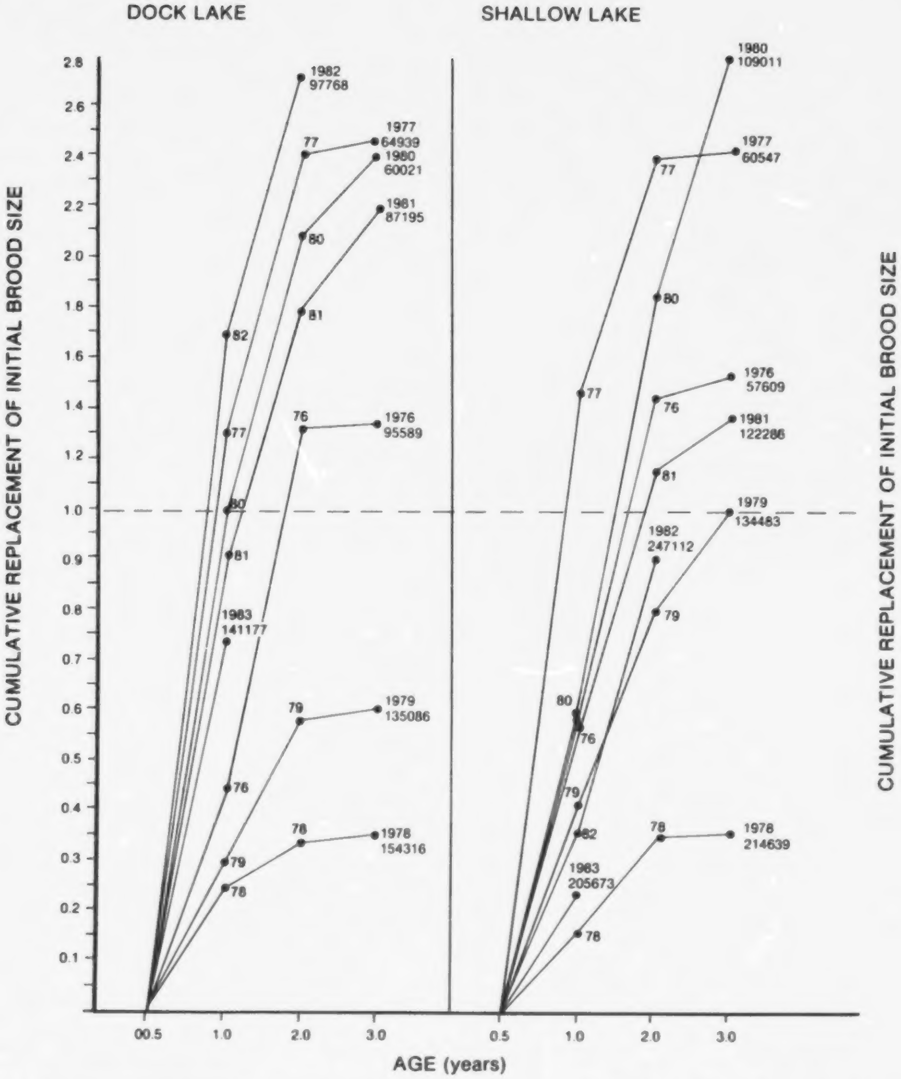

FIG. 9. Cumulative replacement of initial brood size as a function of age in two lakes for four broods of crayfish expressed as a fraction of the initial numbers of each brood. The horizontal dashed line represents exact replacement of the initial number of a brood. Initial brood size is given underneath each year.

0 crayfish in both lakes coincides with their much larger than average G values for those two years (Fig. 1). Lower density might be invoked as the reason for the improved growth in Shallow Lake since there were fewer eggs/m^2 than average. However, this explanation is not borne out in the case of Dock Lake (Table 2). Rather, these data support my previous contention, that the key to the production of large crops of Cambarid crayfish, at least in nutrient rich environments, lies in the occurrence of a favorable thermal regime that promotes rapid molting in juveniles, which in turn then delays the onset of the maturity molt for as long as possible. In nutrient poor habitats, both food supply and thermal regime act in concert to inhibit juvenile growth and so produce individuals that are below average in mean size. We therefore come to the first question posed at the beginning of this report. Can crayfish stocks be overexploited?

Some data are available for both Cambarids, Astacids, and Parastacid crayfishes in both higher and lower latitudes. For Cambarids at lower latitudes, both *Procambarus clarkii* and *P. acutus* have been shown to sustain very intense levels of harvest exceeding 2000 kg/ha (Momot and Romaine 1983). In fact if not intensively fished, *Procambarus* populations tend to stunt due to continuous multiple recruitment of cohorts resulting in an exhaustion of food supply (Romaire 1976; Momot and Romaire 1983).

Astacid crayfishes are better adapted to northern environments (longer life span, many more age-classes, larger size, higher fecundity, larger eggs, and young, and different somatic growth-lipid storage relations which

TABLE 3. Life tables for 5 cohorts of the crayfish, *Orconectes virilis*. Data presented as: age specific survivorship rate (1_x), age specific fecundity rate (m_x) and absolute numbers (N_x) for 5 consecutive cohorts of female crayfish in two lakes. Age of the crayfish (x) is given in years. Ro = 1_xm_x represents the net increase per generation. N_xm_x represents Ro in absolute numbers of eggs produced in a cohort.

	Brood year					
	x	1_x	m_x	1_xm_x	N_x	N_xm_x
Dock Lake						
1976	0	1.00000				
	0.5	0.04928			4 711	
	1.5	0.00993	45.23	0.44933	949	42 942
	2.0	0.00970	90.95	0.88222	927	84 310
	3.0	0.00032	75.90	0.02439	30	2 277
				Ro = 1.35594		129 529
1977	0	1.00000				
	0.5	0.044777			2 907	
	1.5	0.02314	57.10	1.32129	1 503	85 821
	2.0	0.01489	74.10	1.10335	967	71 588
	3.0	0.00062	95.00	0.05852	40	3 800
				Ro = 2.48316		161 209
1978	0	1.00000				
	0.5	0.02887			4 455	
	1.5	0.00656	37.95	0.24895	1 013	38 443
	2.0	0.00218	43.25	0.09428	336	14 532
	3.0	0.000097	137.50	0.01333	15	2 063
				Ro = 0.35656		55 038
1979	0	1.00000				
	0.5	0.04644			6 273	40 782
	1.5	0.00622	48.55	0.30101	840	39 011
	2.0	0.00304	95.15	0.28925	410	3 757
	3.0	0.00019	144.50	0.02745	26	
				Ro = 0.61771		83 550
1980	0	1.00000				
	0.5	0.039853			2 392	
	1.5	0.014762	74.35	1.09756	886	65 874
	2.0	0.010013	111.47	1.11615	601	66 993
	3.0	0.00237	110.37	0.26111	142	15 672
				Ro = 2.47482		148 539
1981	0	1.00000				
	0.5	0.022478			1 960	
	1.5	0.016778	55.6	0.93285	1 463	81 342
	2.0	0.009358	95.0	0.88901	816	77 520
	3.0	.004151	112.2	0.46574	362	40 616
				Ro = 2.28760		199 478
Shallow Lake						
1976	0	1.00000				
	0.5	0.09009			5 190	
	1.5	0.00896	60.75	0.54432	516	31 347
	2.0	0.00849	106.10	0.90079	489	51 883
	3.0	0.00670	150.53	0.10073	39	5 863
				Ro = 1.54585		89 093
1977	0	1.00000				
	0.5	0.10480			6 350	
	1.5	0.02219	66.75	1.48118	1 344	89 712
	2.0	0.01605	58.65	0.94157	972	57 008
	3.0	0.00048	45.80	0.02198	29	1 328
				Ro = 2.44473		148 048
1978	0	1.00000				
	0.5	0.02152			4 620	
	1.5	0.00414	39.85	0.16498	888	35 386
	2.0	0.00351	53.55	0.18796	753	40 323
	3.0	0.00010	109.45	0.01127	22	2 408
				Ro = 0.36421		78 117
1979	0	1.00000				
	0.5	0.12998			1 748	
	1.5	0.01149	36.85	0.42362	1 546	56 970
	2.0	0.00605	55.00	0.33291	814	44 770
	3.0	0.00209	126.00	0.26422	282	35 532
				Ro = 1.02075		137 272
1980	0	1.00000				
	0.5	0.019035			2 075	
	1.5	0.013632	44.45	0.60594	1 486	66 502
	2.0	0.012788	97.80	1.25067	1 394	136 333
	3.0	0.009889	103.50	1.02352	1 078	111 573
				Ro = 2.88013		314 408
1981	0	1.00000				
	0.5	0.010557			1 292	
	1.5	0.008416	70.0	0.58912	1 030	72 100
	2.0	0.008040	70.86	0.56971	984	69 726
	3.0	0.004004	45.0	0.18018	490	22 050
				Ro = 1.33901		163 876

are matched to extended periods of hibernation, etc.). Yet in southern environments they seem quite resilient to exploitation. In the Sacramento delta (California) populations of *Pacifastacus lenuisculus* sustain overall exploitation rates of 28% and up to 49% in areas where the population is abundant. The population apparently adjusts to fishing by varying the age of sexual maturity of females from 1 + to 4 + years with no apparent increases in growth or fecundity (McGriff 1983).

At lower latitudes populations of Parastacids withstand very high exploitation rates. Morrissy (1978) reported that an intense sport fishery for *Cherax tenuimanus* produced stable yields even though the catch per unit effort is low.

At northern latitudes, Astacids seem to be quite resilient. Long term stable yields are reported for an *Astacus astacus* fishery in Lake Steinsfjorden, Norway, at exploitation rates of up to 70% (Qvenild et. al. 1982). The rate was increased to 90% in 1980–81. The short term (1 year) effect was a decline in total catch, catch per unit of effort, and recruitment. Remarkably, neither adult mean length nor increment per molt have changed appreciably since 1942, when mean length was first recorded. Long-term fecundity data are not available, but the number of attached eggs per female are not appreciably different in this population than in other Scandinavian populations. Whether the recent increase from 70 to 90% will produce a noticeable long-term change is unknown. However, the fraction of mature females has decreased to about 10% in crayfish over 70 mm. Whereas the length at maturity increased from 70 mm in 1983 to 78 mm in 1984 (J. Skurdal, personal communication). Apparently at the 90% removal rate, this Astacid population may be now subject to recruitment overfishing.

At present it seems that Astacids can withstand moderate exploitation at higher and intense exploitation at lower latitudes. Cambarids and Parastacids seem to withstand high exploitation at low latitudes and as this study shows moderately intensive rates of removal at high latitudes. Provided that habitat remains intact, Cambarids are extremely resilient and self-regulating. Seemingly the use of stationary gear (traps) removes crayfish that die anyway; therefore, removal rates of 50% of the adult population will have little short-term effect on the population. It appears that fishing mortality may simply substitute for natural mortality as fishing effort increases, at least to the 50% level.

What happens when effort reaches beyond the 50% rate remains to be investigated. It could be that Cambarinid crayfish are susceptible to recruitment overfishing at levels below that recorded for *Astacus astacus*.

This brings us to our second question: can we detect recruitment overfishing if it does occur? Lack of a dramatic growth or fecundity response seems characteristic of most adult crayfish populations when intensively fished, be they Cambarids or Astacids. However, the lack of such a response places populations in higher latitudes relative to those in lower latitudes at a much higher risk. If a succession of years displaying poor climatic conditions should coincidentally occur while a stock is suffering from recruitment overfishing, stock collapse would be inevitable. Since neither a growth nor a fecundity response characteristic of growth overfishing can be easily detected, an exploited stock could pass directly and rapidly into a recruitment overfishing phase. Superficially, the Dock Lake population seemed to manifest some of the symptoms of recruitment overfishing: i.e. lower recruitment (1980–81) (Table 3); decreasing annual production until 1981–82 (Fig. 3), lower numerical yield per unit effort until 1981 (Fig. 4), and poor growth response (Fig. 1). However these early trends did not continue and cannot be attributed to fishing. Furthermore, the unfished population not only manifested many of the same responses found within the last cohort of the exploited stock, but recruitment and annual production have remained below that of the exploited stock.

Seemingly then we cannot determine within an acceptable degree of certainty a priori whether the additional increment in the exploitation rate did or did not reduce stock size below some replacement level. What then are the alternatives? Van Winkle (1977) suggested establishing extensive, long-term monitoring programs, which would allow, with warnings, total exploitation to increase until a posteriori we had "hard data" indicating overexploitation, which would be followed by a reduction in total exploitation and/or a stocking program.

This study suggests that even under the best conditions, hard data in terms of responses to exploitation may be difficult to obtain. Furthermore, if both short- and long-term responses exist and differ in nature, measurement of the latter, as this study suggests, may require a very long time series spanning several generations before definitive trends are established. Van Winkle suggested that a 10-year span was insufficient to detect a real reduction in population size of fish due to exploitation in temperate/southern climatic conditions. In the case of the relatively short-lived crayfish, *Orconectes virilis*, 8 years of data were insufficient.

Given the complex interplay of environmental impacts, masking the effects of exploitation, development, and application of increasingly complex stock-recruitment or MSY models for crayfish is probably futile. Can we develop or devise an alternate or modified management regime for crayfish? The much heralded alternative of subsuming lake individualities into an overall ecosystem model that can deal with the commonalities found in lake sets (Holling 1973; Regier and Henderson 1973) has serious limitations. The critical ecosystem level concepts described and questions asked so far have not provided realistic answers of certainty sufficient for decision making. The dilemma is that most of the concepts thus far invoked, e.g. resilience, stability, index of well-being, persistence, community structure, community response (Regier 1977), seem not, at least to date, to be operationally definable, since they cannot at present be quantified and a qualitative response is not sufficient to deal with the problem. Real progress may not be possible until we develop useful operational definitions for these concepts. We must realize that this will be a long involved process involving the accumulation of costly, unfashionable, well-documented, long-term experimental management studies. Such studies may provide the empirical data base necessary to clarify and define these concepts.

Lindquist (1977) advocates an empirical strategy maximizing survival of both the exploited stock and the fisherman. Rigler's (1982) empirical approach may provide the most appropriate paradigm for development of a predictive science for the management of crayfish populations.

At our present level of understanding, removal rates of 50% for Cambarids and 70% for Astacids seem to give long-term stable yields and so provide a reasonable conservative empirical estimate until additional evidence is gathered.

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Use of Catch and Effort Data for Parameter Estimates for the Loco (*Concholepas concholepas*) Fishery of Central Chile

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The fishery for loco, *Concholepas concholepas*, is examined for three areas in central and northern Chile. Annual variation in catch per unit of effort and estimation of catchability, natural mortality, and recruitment parameters are discussed.

Results of a modified Delury model providing estimates of daily recruitment and natural mortality, in addition to catchability, are presented. Results of this model are compared to results suggested by cohort analysis of length frequency data. Implications for the management of the loco fishery are discussed.

On examine les activités de pêche à la limace de mer (*Concholepas concholepas*) pour trois secteurs situés au centre et au nord du Chili. On discute des variations annuelles des prises par unité d'effort et de l'estimation des paramètres suivants: possibilité de capture, mortalité naturelle et recrutement.

On présente les résultats obtenus à l'aide d'un modèle modifié de Delury, qui fournit une estimation de la mortalité naturelle et du recrutement quotidiens ainsi que la possibilité de capture. Les résultats de ce modèle sont comparés aux résultats fournis par une analyse par cohortes des données sur la fréquence des longueurs. On discute des incidences de l'étude sur la gestion de la pêche de la limace de mer.

Introduction

The fishery for loco, *Concholepas concholepas*, is an artisan fishery which has not previously been well documented. Catch statistics were available for a number of years, but not data for fishing effort. In June 1983, the Grupo de Ecología Marina of the Universidad Católica de Chile started taking daily catch and effort data for fishing villages in central Chile. Catch and effort data were also obtained for two villages in north central Chile.

Few models are available for management of fisheries with only one or two years catch and effort observations. Tagging studies or growth studies, especially in conjunction with age or length data, may yield valuable information on population dynamics. However, estimates of recruitment and mortalities from catch statistics generally require many years of data. The problem is particularly acute in many invertebrate fisheries where ages are not easily determined.

Our analysis includes three areas for which at least a full nine month season of catch and effort data were available. Our objective was to examine models which would provide estimates of important population parameters with only catch and effort data.

The loco inhabits the intertidal and litoral zone, and ranges from Peru to the Cape Horn (Stuardo 1979) with most of the fishery located in central and northern Chile. Most of the artisanal fishery operates from open boats with one or two divers working at depths of 4–25 m. Locos are legally recruited into the fishery at a length of 100 mm and, starting in 1982, could be legally caught in central and northern Chile only from June 1 through February 28 of the following year (Castilla and Jerez 1986). Previously there was no closed season.

Summaries of loco reproduction by Ramorino (1979) and Castilla (1979) indicate that sexual maturity is reached at approximately 5 cm. Although reproduction occurs principally in the summer and autumn months (December through May), egg mass placement has been observed all year.

Models

Models examined were all derived from the general model

$$N_{t+1} = N_t e^{-qf_t - M} + R \quad (1)$$

where N_{t+1} and N_t are the numbers of individuals in the fishery at time $t+1$ and time t, respectively, and f_t is the fishing effort at time t. Coefficients of catchability, q, natural mortality, M, and recruitment, R, are assumed to be constant during the interval.

Two models which estimate the rate of fishing success from short term catch and effort statistics were initially examined. The Delury method (Ricker 1975) given by

$$(2) \qquad \ln(C/f)_t = \ln(C/f)_0 - qE_t$$

describes the relationship between catch per unit effort and cumulative effort, E_t. This model is derived from equation (1) by assuming M and R to be negligible ($=0$), multiplying the equation by q to convert N to C/f ($qN = C/f$) and then taking the logarithm. The equations to calculate C/f at time $= 1, 2, \ldots, t$, are

$$\ln(C/f)_1 = \ln(C/f)_0 - qf_0,$$

$$\ln(C/f)_2 = \ln(C/f)_0 - qf_0 - qf_1,$$

and

$$\ln(C/f)_t = \ln(C/f)_0 - q\sum_{i=0}^{t-1} f_i = \ln(C/f)_0 - qE_t$$

respectively, which corresponds to the Delury equation (2).

The Leslie method (Ricker 1975) is given by

$$(3) \qquad (C/f)_t = (C/f)_0 - qK_t$$

which fits the relationship between catch per unit of effort (C/f) and cumulative catch, K_t. This model follows from equation (1) after muliplying by q, assuming that $M = 0$ and $R = 0$, and using the approximation $e^x = 1 + x$. In consequence, $e^{-qf}t$ is approximated as $1 - qf_t$ (Chien and Condrey 1986). At this point the model is

$$(C/f)_{t+1} = (C/f)_t\,(1 - qf_t)$$

or

$$(C/f)_{t+1} = (C/f)_t - qf_t(C/f)_t = (C/f)_t - qC_t.$$

Redefining the time periods from t_0 to time t, as with the Delury method, and employing the summation

$$K_t = \sum_{i=0}^{t-1} C_i$$

one obtains (3).

The summation of catch over time is discussed by Braaten (1969), who recommends that calculations to the midpoint of the last time interval be included in calculations of K_t. However, our use of daily catch data would seem to reduce the necessity of including half intervals. In our calculations, summations used (to $t-1$) provided better fits to the data than summations incorporating half of the last interval.

Another version of the basic model (1) has been examined by Chapman (1974) and by Breiwick (1978) in applications to whale stocks. Their version, termed a modified Delury model, does not require assumptions of zero natural mortality and zero recruitment as does the Delury model. However, their adaptation does require a prior estimate of the natural mortality and an assumption of constant recruitment.

We propose another modification of the Delury model, a three parameter model which does not require a prior estimate of natural mortality. Our derivation is identical to that previously described for the Leslie method, except that M is not assumed to be zero. The transformation used for the Leslie model gives $1 - qf_t - M_t$ as an approximation of the exponential portion, $e^{-qf_t - M_t}$. As with the modified Delury model of Chapman (1974) and Breiwick (1978), the recruitment term is retained. Multiplication by q and conversion to a summation equation, as for the Delury and Leslie methods, gives the equation,

$$(4) \qquad (C/f)_t = (C/f)_0 - q\sum_{i=0}^{t-1} C_i - m\sum_{i=0}^{t-1} (C/f)_i + qr\,(t-1).$$

Lower case characters "m" and "r" were employed to indicate our use of daily rates of natural mortality and recruitment, respectively. Upper case M and R were reserved to describe annual rates.

The modified model employs time as a variable, and two additional variables which are cumulative. These variables all increase over time, and strong correlations between the variables are likely for this model. These correlations could result in multicolinearity. Several criteria are available for determining whether multicolinearity exists in a data set. Criteria outlined by Belsley et al. (1980) suggest the use of a coefficient index, CI, based on the maximum and minimum eigenvalues (λ) calculated from a standardized sum of squares and cross products matrix. The coefficient index ($\mathrm{CI} = \sqrt{\lambda_{max}/\lambda_{min}}$) indicates strong multicolinearity when between 30 and 100. Montgomery and Peak (1982) use the critical value of 30 recommended by Belsley et al. (1980), while Hocking and Pendleton (1983) suggest that 30 may sometimes be too small as a critical value. We have used a condition index value of 30 as the criteria for the presence of multicolinearity.

Montgomery and Peak (1982) outline three courses of action generally used to address multicolinearity: (1) simplify or modify the model, (2) obtain more data, or (3) use ridge regression techniques. There are a number of ways to simplify or modify the model. Either m or r could be assumed to be zero, and omitted from the model. Extreme simplification (both m and r equal zero) of equation (1) would result in either the Leslie or Delury methods mentioned earlier. The model used by Chapman (1974) and Breiwick (1978) is also a simplified version of the model.

The second approach, obtaining more data, would probably be the best solution, but is impractical in many situations. Also, the assumption of constant recruitment may be more difficult to meet for a longer time period.

The third solution to multicolinearity is ridge regression. This technique may provide adequate results when more data cannot be obtained. Multicolinearity generally causes parameter estimates whose absolute values are too large. Montgomery and Peak (1982) state that parameter estimate magnitudes and signs contrary to expectations suggest muticolinearity. Ridge regression involves a stabilizing transformation, adding a constant *K* to the main diagonal of the sum of squares and cross product matrix, which will reduce the absolute value of all parameter estimates (eventually driving them to zero as *K* increases). The new estimates will be biased, the magnitude of the bias depending on the value of *K* used.

Ridge regression provides a series of parameter estimates, corresponding to different values of *K* used. Criteria for determining the appropriate value of *K* dictate that the value added should be as small as possible, to reduce bias in the parameter estimates, but should be sufficient to stabilize the estimates.

We will examine some of these approaches in fitting equation (4). For one fishing area with a single season of data, we will examine the results of ridge regression. For two areas with two or more years of data, we examine the effect of having a larger data base.

All regressions, including ridge regressions, were weighted by the daily effort (*f* in boat days) used in calculating the dependent variable (C/f). Models considered for the single season areas were the Leslie and Delury methods, and the model given in equation (4). Ridge regressions were also run for the modified model when the condition index exceeded 30. The original model (equation 1) was also fitted with nonlinear techniques for comparison. Signs were not specified in fitted models; the expected signs were negative for *q* and *m*, and positive for *r*. All statistical models were fitted using SAS (SAS 1982, 1983).

The Fishery

Our assumptions include that of constant recruitment made by Chapman (1974) and Breiwick (1978). Data used for the Cruz Grande area (Fig. 1) indicate a long period of stable, though variable, catch per unit of effort prior to 1982. We assume that this stability would provide a relatively constant rate of recruitment over the period examined. Events after 1982 will probably effect recruitment, but not until the 1985 season or later. Data prior to 1982 was not available for the Hornos area, but this area is adjacent to Cruz Grande, and we assume its exploitation has followed a pattern similar to Cruz Grande.

The short period examined for the Quintay area (9 mo) should preclude the effect of annual changes in recruitment. Reproduction peaks in summer and autumn months (December through May), but since egg mass placement does occur all year, we have assumed that recruitment is constant during the season.

Another assumption is that exploitation is haphazard, and that *C/f* is representative of mean densities of locos. Since the loco is somewhat sessile, it is possible that a methodical exploitation of the fishing grounds could artificially maintain catch rates in spite of diminishing stocks. However, our study and discussions with fishermen indicate that no coordination of exploitation exists between the fleet, and that fishermen will return to previously harvested areas in as little as 2-4 wk. Therefore, this assumption should be adequately met by application of the model to longer

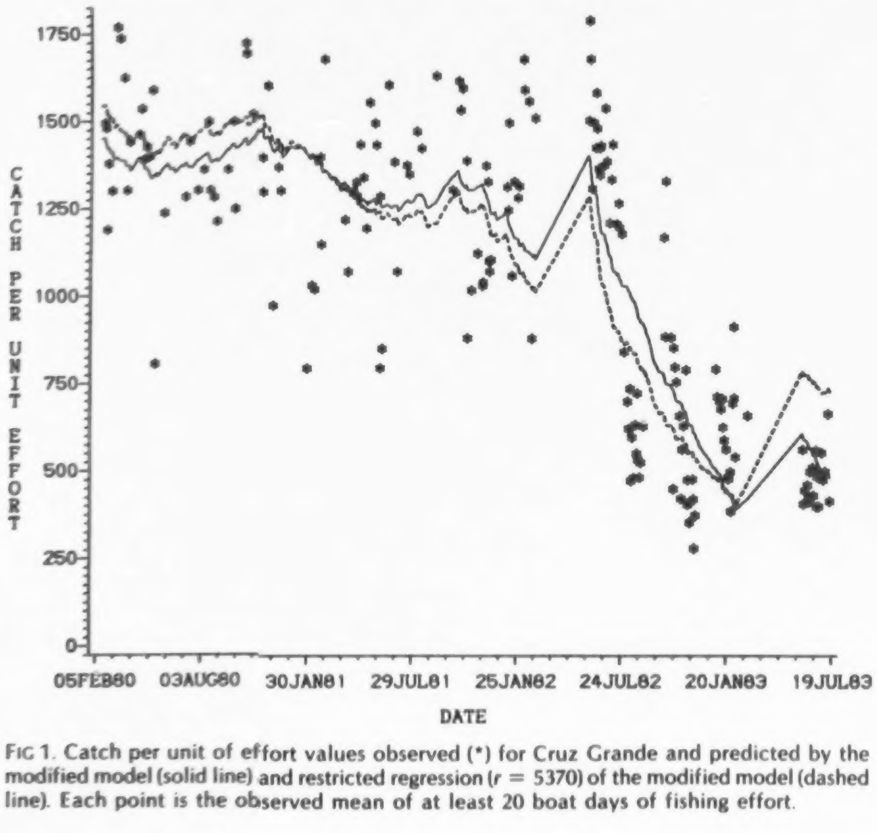

FIG 1. Catch per unit of effort values observed (*) for Cruz Grande and predicted by the modified model (solid line) and restricted regression ($r = 5370$) of the modified model (dashed line). Each point is the observed mean of at least 20 boat days of fishing effort.

periods of catch and effort data.

The fishing village of Quintay (see map, Castilla and Jerez 1986) had the most complete and reliable data base among those areas examined. Segments of information were missing from two areas with longer data histories, Hornos and Cruz Grande. When both catch and effort were missing for these areas, the number of fishing days and average daily effort was estimated from adjacent periods. Given catch or effort, the remaining variable was estimated from mean catch per unit effort for adjacent periods. Values estimated in this manner were not used in fitting regression equations, but were used to determine values of ΣC and $\Sigma(C/f)$ used as independent variables (equation 4).

Examinations of the data revealed that extremely high catch per unit effort often occurred for the first two or three days of the season. Investigation at the start of the 1984 season revealed that fishermen would stockpile locos in days preceding the season opening, and land them in the first few days of the season. For this reason, the first 3 d of the 1983 season in Quintay (Fig. 2) and the first 2 d of the 1983 season in Hornos (Fig. 3) were not used in fitting the regression equations, but were included in values ΣC and $\Sigma(C/f)$ used as independent variables (equation 4). No obvious excessive landings occurred for opening days in the Cruz Grande area (Fig. 1).

Model Evaluation

Leslie and Delury methods were applied to Quintay only, and both fits were statistically significant ($\alpha = 0.05$). Even the single season of data available for this area is probably too long a period for the assumptions of negligible M and R to be met, and the data does not indicate a sustained decrease in rate of catch. The estimate of catchability (q) from the Delury method was positive (Table 1), and not considered further. Parameter estimates for the Leslie model (Table 2) appeared to be low ($F = 0.327$). Analysis of length frequency data (Castilla and Jerez 1986) indicate the total annual mortality ($Z = F + M$) for Quintay should be approximately 1.876. The carnivorous Loco has a high trophic level, so the fishing mortality was expected to be the major component of total mortality. The estimate of 0.327 appears to be an underestimate.

The modified model was statistically significant ($\alpha = 0.05$), and appears to fit the observed data well (Fig. 2, solid line). However, for Quintay the estimate for fishing mortality is excessive ($F = 7.599$) as is that of natural mortality ($M = 1.866$) (Table 2). Results of the nonlinear fit (Table 1) did not appear to be superior to the modified model. The parameters q and r appeared to be underestimated, while m was positive.

Failure of the modified model to provide satisfactory results for Quintay was partly attributed to linear dependencies between variables. Condition index (CI) values given in Table 1 for the modified model show that the least indication of multicolinearity is present for Hornos (CI = 17), and greatest for Quintay (CI = 72). Only Quintay exceeded the criteria of 30. K values from 0 to 0.3 were used in ridge regression, at 0.0001 intervals, and examined for stabilization. Table 3 shows a sample of the values of parameter estimates for

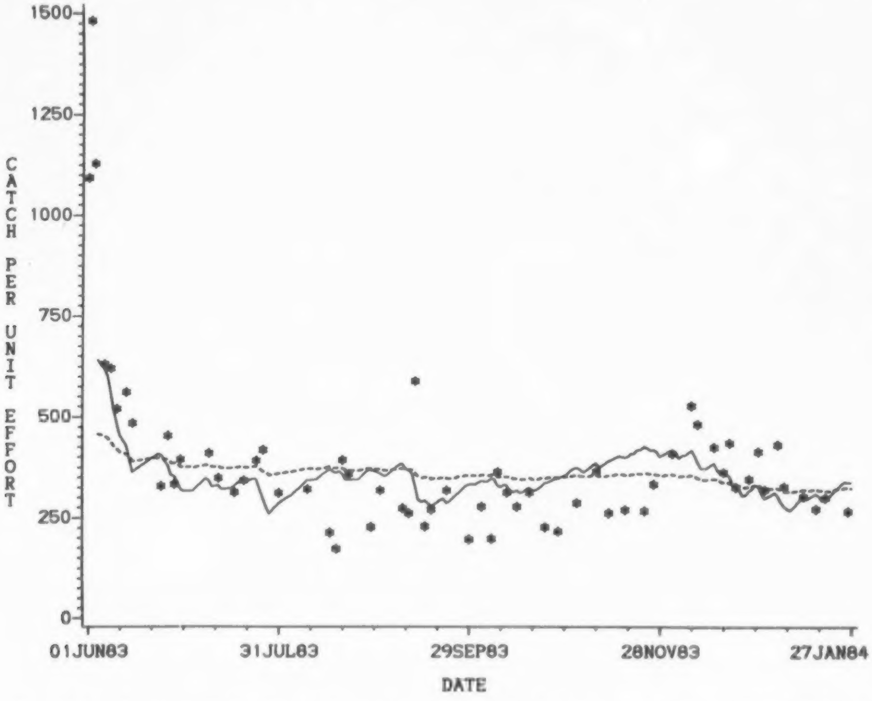

FIG. 2. Catch per unit of effort values observed (*) for Quintay and predicted by the modified model (solid line) and ridge regression of the modified model (dashed line). Each point is the observed mean of at least 20 boat days of fishing effort.

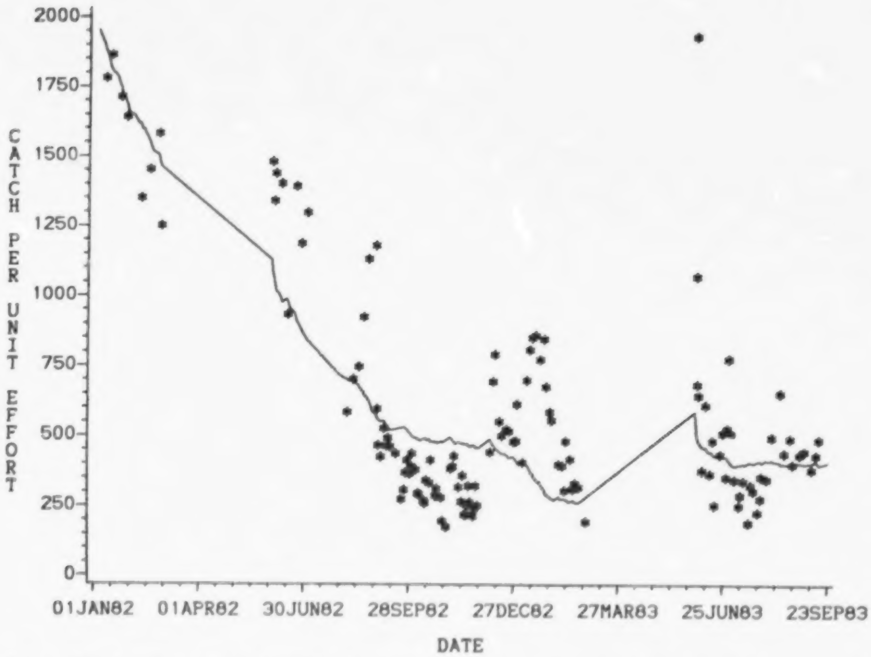

FIG. 3. Catch per unit of effort values observed (*) for Hornos and predicted by the modified model (solid line). Each point is the observed mean of at least 20 boat days of fishing effort.

TABLE 1. Parameter estimates and standard errors from various models employing catch and effort data for three fishing areas in central and northern Chile. Underlined values were not statistically significant (H_0:Parameter = 0, $\alpha = 0.05$).

Area and model	Intercept	$q(10^{-3}) \pm$ SE(10^{-3})		$m(10^{-3}) \pm$ SE(10^{-3})		qr	± SE	R^{2a}
Quintay (n = 205)								
Leslie	431.83	−0.196	0.061	—		—		0.048
Delury	5.36	+0.043	5.891	—		—		0.208
Nonlinear	701.62	*−2.376*	1.677	*0.800*	10.691	1.470	0.090	—
Modified (CI^b = 72)	957.63	−4.548	1.169	*−1.865*	11.612	9.103	2.309	0.211
Ridge (K = 0.0118)	530.20	−1.034	0.167	*−0.402*	0.595	1.790	0.323	—
Hornos (n = 319)								
Nonlinear	1866.35	−2.451	0.273	*0.753*	0.692	0.809	0.033	—
Modified (CI^b = 17)	1938.46	−0.736	0.171	−7.052	0.467	4.764	0.596	0.613
Cruz Grande (n = 444)								
Nonlinear	1394.76	−1.114	0.148	3.770	0.538	0.327	0.043	—
Modified (CI^b = 26)	1451.17	−0.672	0.060	1.450	0.203	1.155	0.424	0.649
Restricted (r = 5370)	1545.84	−0.726	0.066	−0.531	0.034	3.897	fixed	0.572

[a] Coefficient of multiple determination.
[b] Coefficient index ($\sqrt{\lambda_{max}/\lambda_{min}}$.

Quintay with increasing K. Values appear to stabilize quickly, and at a value of K = 0.01 most change has been completed.

One additional criteria for K selection was employed for Quintay. Since the value of Z was independently estimated as 1.876 (Castilla and Jerez 1986), parameter estimates from ridge regression were examined to find a combination such that ($Z = F+M = 365^*m+q^*E_{365} = 1.876$), where E_{365} is the total effort for the most recent 365-d period in the data set. The best value of K by these criteria was 0.0118, and those parameter estimates are included in Tables 1 and 2. The C/f estimates produced by the modified model fitted with ridge regression are graphed in Fig. 2 (dashed line).

Although the ridge regression result was chosen to provide an estimate of Z consistent with other techniques, those other techniques do not provide a subdivision of Z into its component parts, F and M. The component parameter estimates for Quintay, F = 1.727 and M = 0.147, appear to be reasonable for this species. Cohort analysis (Castilla and Jerez 1986) provided similar results for fishing mortality.

Daily recruitment for Quintay, estimated as the coefficient qr (1.790) divided by the estimate of q (0.001034), was of 1732 individuals per day. This is consistent with Cohort analysis results (Castilla and Jerez 1986) which indicated that 218 784 pre-recruits (9.5–10 mm) would grow into the fishery in 0.351 yr dur-

TABLE 2. Estimates of Loco population parameters derived from statistical models of catch and effort data for three fishing areas in central and northern Chile. The parameter F is calculated as q^*E_{365}, employing the observed effort for the most recent 365 day period in the data set.

Area and model	$N_0{}^*10^6$	F	M	Daily r
Quintay				
Leslie	2.2062	0.327	—	—
Delury	—	—	—	—
Nonlinear	0.2954	3.968	+	619
Modified	0.2106	7.599	1.866	2002
Ridge	0.5130	1.727	0.147	1732
Hornos				
Nonlinear	0.7621	6.188	+	330
Modified	2.6346	1.859	2.574	6474
Cruz Grande				
Nonlinear	1.2520	3.294	+	293
Modified	2.1599	1.987	+	1720
Restricted	2.1299	2.146	0.194	5370

TABLE 3. Values of parameter estimates for selected values of K resulting from ridge regression applied to data for the Quintay area. The equation used was $(C/f)_t = (C/f)_0 + qK_t + m\Sigma(C/f) + qr\,(t-1)$.

Value of k	Intercept	q	qr	m
0.000	957.63	−0.00455	9.103	−0.001866
0.002	749.51	−0.00287	5.429	−0.000617
0.004	656.22	−0.00209	3.872	−0.000486
0.006	603.52	−0.00165	2.999	−0.000442
0.008	569.66	−0.00136	2.440	−0.000421
0.010	546.06	−0.00117	2.051	−0.000409
0.0118	530.20	−0.00103	1.790	−0.000402
0.012	528.67	−0.00102	1.765	−0.000401
0.014	515.32	−0.00091	1.545	−0.000396
0.016	504.75	−0.00082	1.372	−0.000391
0.018	496.17	−0.00075	1.231	−0.000388
0.020	489.06	−0.00069	1.115	−0.000386
0.025	477.97	−0.00060	0.896	−0.000382
0.030	466.31	−0.00050	0.743	−0.000379

ing the 1983/84 season. This number would be reduced by natural mortality, but the daily rate of 1708 locos per day is similar to the figure obtained by ridge regression. Quintay was the only area for which independent estimates of recruitment were available.

Modified model fits for areas with longer data histories showed little indication of multicolinearity as judged by condition indices (Table 1), and ridge regression was not used. The fits were significant for both Hornos and Cruz Grande ($\alpha = 0.05$). No independent estimates of parameters were available for comparison. However, estimates of q from the modified model did not appear excessive, as it was for Quintay. Fishing mortality, F, was estimated to be 1.859 and 1.987 for Hornos and Cruz Grande respectively (Table 1). These would appear to be reasonable for the loco fishery, and are consistent with ridge regression estimates for Quintay.

Although results of regression analysis for Hornos and Cruz Grande did not indicate strong multicolinearity, there are still correlations between independent variables. Another possible manifestation of this occurs in the form of non-identifiable variables, where two variables vary together in a compensating manner (e.g. one variable increases while another decreases). Cruz Grande displayed a positive m estimate for the modified model while the estimate of r was small. The reverse was true for Hornos, with a small value of m and a large value of r. When this occurs the approach employed by Chapman (1974) and Breiwick (1978) may be preferable. However, the model we have used allows the user to fix any of the parameters, rather than only the natural mortality parameter.

For example, during a stable period of catch in Cruz Grande from 2/13/1980 through 2/28/1982 there were 4 011 697 locos taken. If we assume that this rate of 5370 locos per day was approximately equal to recruitment, and fix recruitment at this value, the remaining parameters may be estimated by linear techniques. Estimates for N_0 and q (Table 1) change relatively little, while m changes considerably and becomes negative. The resulting estimate for M (0.194), is similar to the estimate for Quintay.

The results suggest that the modified model may be useful in providing estimates to the parameters, but that large deviations from reasonable estimates are also possible due to correlations and linear dependencies inherent between the variables. Evaluation of the fit provided by the model should therefore be supported by estimates from other sources, such as values from length frequencies. Ridge regressions or restrictions on the parameters may be required to obtain adequate results.

Evaluation of the Fishery

Both the model fitted in this paper and Cohort analysis (Castilla and Jerez 1986), indicate the importance of recruitment to the fishery. Rates of recruitment for Quintay indicate that additions to the fishery through recruitment were of the same magnitude as the initial population ($N_0 = 450578$, $R = 645579$). There does not appear to be a sufficiently large stock to buffer a recruitment failure. Since catches for the same period were approximately equal to recruitment ($\Sigma C = 651895$), it is apparent that the fishery is stable at the moment, but very dependent upon recruitment.

No information is available for Quintay prior to the 1983/84 fishing season. However, evidence from Cruz Grande and Hornos indicates there was a large increase in effort in the 1982/83 season. Effort nearly tripled in the Cruz Grande area (Table 4), and catch per unit effort decreased drastically (Fig. 1). Catches of 1.881×10^6 in the 1980/81 season and 1.513×10^6 in the 1981/82 season were exceeded in the 1982/83 season with a total catch of 2.443×10^6 locos. The latter catch probably exceeded recruitment, reducing the standing stock. Although recruitment in the next few years will reflect stock levels prior to the 1982/83 season, recruitment may eventually be reduced due to diminished stock available for reproduction. It seems imperative that

TABLE 4. Mean fishing effort in boat days applied to three areas of the Loco fishery of central and northern Chile.

Fishing area	Period		Total effort	Days	Mean effort	
	Starting	Ending			Season	Annual
Cruz Grande	2/13/80	5/31/80	433	108	4.01	
	6/ 1/80	5/31/81	1388	365	3.80	3.80
	6/ 1/81	2/28/82	1157	273	4.24	3.17[a]
	6/ 1/82	2/28/83	3038	273	11.13	8.32[a]
	6/ 1/83	8/31/83	945	90	10.50	
Hornos	1/ 1/82	2/28/82	164	57	2.88	
	6/ 1/82	2/28/83	2521	273	9.23	6.91[a]
	6/ 1/83	10/31/83	1289	152	8.48	
Quintay	6/ 1/83	2/28/84	1671	273	6.12	4.58[a]

[a] Includes 92-d closed season with no effort.

loco stocks be studied in view of the changing stock levels to insure that present levels are capable of maintaining historic rates of recruitment.

Another result suggested by the model is that the rapid decline in *C/f* observed in Cruz Grande in the 1982/83 season can be explained entirely by increased effort (Table 3). The restricted model (Table 1) employs a moderate natural mortality term, and tracks the observed data well. In contrast, the model fitted to the Hornos area, gives a large term for natural mortality (Table 1). It seems likely that this fit would benefit from restrictions placed on parameter estimates, but no estimates were available.

An anomaly was noted in the catch rate for all three areas (Fig. 1–3). There was often an increase in catch per unit effort in December, and a subsequent decline in January, which was not explained by the model. We believe this is attributable to changes in Loco behavior at the onset of the breeding season. Additional investigation is required to document this occurrence and improve parameter estimates.

Discussion

The modified model examined appears to provide reasonable estimates to some parameters when 2 or more years of data are available for the loco fishery. However, other parameters were not well estimated and a prior estimate of one of the parameters was required to restrict the model and produce reasonable estimates. Use of the model to estimate all three parameters would not appear advisable unless independent estimates of at least one parameter are available to confirm the estimates. A single season of data taken under more highly controlled conditions provided good estimates when ridge regression was employed.

Data from areas with two or three years of observations indicate that the loco fishery experienced a large increase in effort in the 1982/83 season. The increased effort was accompanied by a sharp decline in the catch per unit effort. The model indicates that for Cruz Grande, which has the longest data history, the decline in catch per unit of effort is attributable to increased effort.

The effect of declining stocks on future recruitment cannot be evaluated at this time. The loco fishery appeared to maintain small stock levels relative to recruitment and harvest, and will rapidly reflect changes in recruitment. Studies of present reproductive success and recruitment were recommended.

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INVERTEBRATE MODELS

Fishing Effort Standardization in the British Columbia Prawn (*Pandalus platyceros*) Trap Fishery

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A study, designed to determine if depth, length of soak, and diel period are factors which significantly affect the effective fishing effort in the B.C. prawn, *Pandalus platyceros*, trap fishery was carried out in September 1977. Results of the study found that catch per trap changed significantly when depth, soak-time and diel period were varied. These changes in catches were attributed to prawns showing a preference for a deeper water habitat, the relationship between ingress and escapement in baited traps, and changing diel behavior patterns. An analysis of length frequency data found that mean size of prawns were largest in shallowest depths and progressively smaller outward to deeper depths. Since catches in shallower depths were composed mainly of migrating prawns it is speculated that the size difference is a function of the animals ability to migrate, i.e. larger animals move further away from their deeper shelter habitat and are more available in the shallowest depths. Examples are given of how fishermen can use this information in selecting appropriate fishing strategies.

En septembre 1977, on a effectué une étude visant à déterminer si la profondeur, la durée de mouillage et la période nycthémérale constituent des facteurs qui influent sensiblement sur l'effort de pêche réel de la crevette de la C.-B (*Pandalus platyceros*) capturée à l'aide de casiers. Les résultats de l'étude ont montré que les prises par casier fluctuaient de façon appréciable lorsque la profondeur, la durée de mouillage et la période nycthémérale variaient. On a attribué ces changements au fait que ces crevettes vivent de préférence en profondeur, à la relation entre le nombre d'individus entrant dans les casiers appâtés et en sortant, et aux changements dans le comportement nycthéméral. Une analyse des données sur la fréquence des longueurs a montré que la taille moyenne des crevettes était la plus grande dans les eaux les moins profondes et diminuait graduellement à mesure que la profondeur augmentait. Comme les prises dans les secteurs peu profonds comprenaient surtout des crevettes en migration, on émet l'hypothèse que la différence de taille est fonction de la capacité de ces animaux à migrer, c'est-à-dire que les individus plus gros s'éloignent davantage de leur habitat habituel pour se retrouver en plus grand nombre dans les secteurs moins profonds. On donne des exemples de la façon dont les pêcheurs peuvent se servir de cette information pour choisir des techniques de pêche appropriées.

Introduction

Commercial catch and effort data may be used to obtain an index of species abundance. Ricker (1975) reviewed techniques used in analysis of this type of data and described two procedures developed by Leslie and Delury. Ricker pointed out that in both procedures two assumptions must be met before the relationship between catch per unit of effort and stock abundance can be considered valid. The first assumption is that natural mortality and migration are limited to the extent that any decline in abundance, reflected by declining catch per unit effort, is predominantly caused by fishing mortality. Thus, an understanding of natural mortality and migration must be developed so that data being analyzed can be obtained from a time frame over which the effects of these two factors are negligible. The second assumption is that catchability, (the fraction of fish stock caught by a defined unit of fishing effort) is constant.

For industry, catch and effort data can be used to evaluate fishing strategies. Austin (1977) points out that the main goal of industry is to maximize profits which is not necessarily tantamount to maximizing catch per trap day, catch per trap haul or total catch. In this instance, catch and effort provides a measure of relative fishing power for a profit maximization model.

In both instances, catch and effort data must incorporate the variables which significantly affect the fishing process in order to calculate a standardized effective fishing effort. Treschev (1975) noted, however, that most statistical catch and effort data are collected in an arbitrary form and have no scientific basis for claiming to reflect the nature of the fishing process.

A number of authors have speculated on factors which may influence measurement of fishing effort for trap fisheries. Bennett and Brown (1979) suggested that the effectiveness of a baited trap as a unit of effort depends on the relationship of factors relating to the animal's behavioral response to the bait, efficiency of the traps, and environmental conditions. Simpson (1975) discussed effects of trap design, single traps vs strings of traps, bait, skill of the fisherman, and mixed fisheries. Munro (1974), Skud (1979), and Miller (1979) discussed the effects of varying the length of soak-time. Thomas (1958) and Morgan (1974, 1979) considered seasonal environmental and physiological factors, and discussed size and sex influences on vulnerability to capture.

This paper reports on some variables which may affect the definition of effective fishing effort in the British Columbia prawn, *Pandalus platyceros*, trap fishery. This study was designed to determine if depth, length of soak, and diel period are factors which significantly affect the nature of the fishing process either individually or in combination.

Materials and Methods

The study area, located in Howe Sound in southern British Columbia (Fig. 1), was chosen because it provided a population of prawns which was geographically isolated, historically exploited, and previously studied.

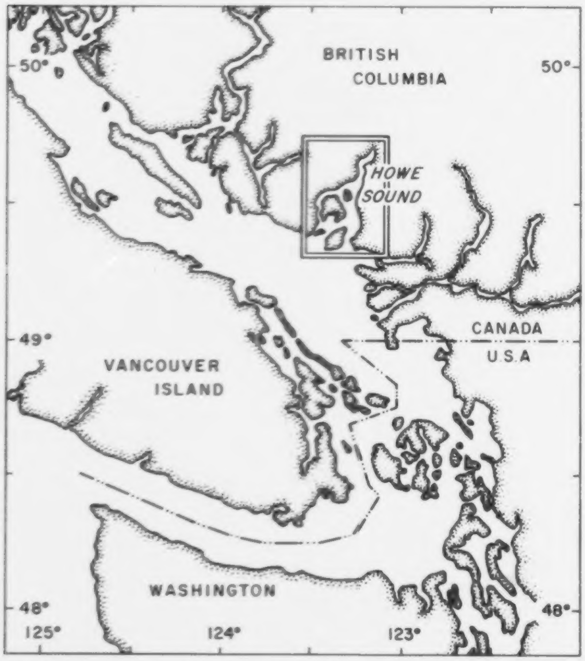

FIG. 1. Site of experiment, Howe Sound, British Columbia.

Three strings of long-lined prawn traps were fished. Each string consisted of ten uniformly constructed prawn traps (Fig. 2) spaced along the groundline at 37 m intervals. Each trap consisted of a four posted cylindrical aluminium frame 56 cm in diameter and 25 cm high covered with 2.8 cm nylon mesh, and fitted with 3 funnel entrances. Strings were set on each of the 27, 55, and 91 m contours. After each haul-back, the traps were freshly baited with herring, and a depth sounder and shore markers were used to reset the gear as close as possible to the same location.

Soak time schedules of 3, 6, 12, and 24 h intervals were fished. Experimental periods commenced at 07:00 and lasted for 24 h. Each soak time schedule was run for two complete experimental periods (Table 1). The study was conducted in September 1977, when dawn and dusk were roughly at 07:00 and 19:00 h respectively.

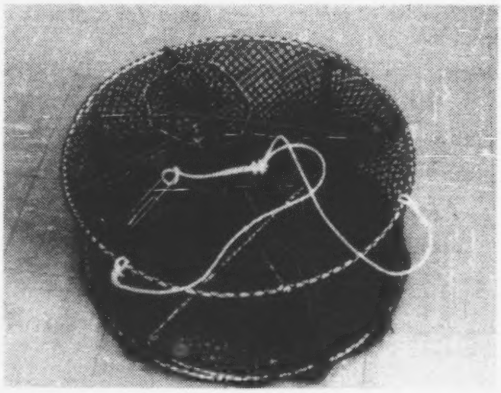

FIG. 2. Prawn trap used for the 1977 effort standardization experiment.

Captured prawns were counted, weighed, sexed, measured in carapace length, and removed from the study area.

Analysis

To compensate for lost traps, the catch data are expressed as the number of prawns per trap hauled. To compare catches for all treatments, the catch/trap hauled data from the experiment were compiled in four ways and analysed using an analysis of variance and covariance program from UCLA Biomedical Computer Program series.

In the first analysis, catches within each soak schedule were compared over a 24-h period. A 2-way analysis of variance was carried out by depth strata and the 4 soak schedules: 3, 6, 12, and 24 h. In a second analysis, the fishing day was divided into 12-h periods. This allowed for a 3-way analysis of variance on catches by depth strata; 3 soak schedules: 3, 6, and 12 h; and diel period. In a third analysis, the fishing day was divided into 6-h periods. This permitted a 3-way analysis of variance on catches by depth strata; 2 soak schedules: 3 and 6 h; and diel period. In a fourth analysis, catches were used from each 3-h diel period. This allowed for a 2-way analysis of variance on the catch rates by depth strata, and diel period.

In addition to the analysis of catch data, an analysis of variance and a length frequency ageing analyses (Schnute and Fournier 1980) were conducted on the length frequency data by depth strata.

Results

Depth strata, soak schedule, diel period and a number of interactions were acting in ways which significantly ($P < 0.05$) affected the prawn catch/trap hauled (Table 2). Catches and catch rates (catch/trap per hour of soak) were lower in the 27 and 55 m depth strata than in 91 m for each soak schedule (Fig. 3). For each depth stratum, the shorter 3 and 6 h soak schedules had consistently higher catches and catch rates than the 12 and 24 h soak schedules (Fig. 3) which is similar to what

TABLE 1. Number of replicate traps hauled for each soak-time and depth interval.

	Soak-time (h)			
Depth (m)	3	6	12	24
27	160	79	40	20
55	160	80	40	20
91	160	79	40	20

TABLE 2. Results of the 4 analysis of variation of catches for fishing periods.

Analysis 1 (catches over a 2-h period)

Source of variation	D.F.	Tail probability
Depth (D)	2	0.0000
Soak schedule (S)	3	0.0000
D×S	6	0.0001
Error	886	

Analysis 2 (catches over a 12-h period)

Source of variation	D.F.	Tail probability
Depth (D)	2	0.0000
Soak schedule (S)	2	0.0000
Time (diel period) (T)	1	0.0018
D×S	4	0.0002
D×T	2	0.0000
S×T	2	0.0639
D×S×T	4	0.0138
Error	820	

Analysis 3 (catches over a 6-h period)

Source of variation	D.F.	Tail probability
Depth (D)	2	0.0000
Soak schedule (S)	1	0.0000
Time (diel period) (T)	3	0.0021
D×S	2	0.0018
D×T	6	0.0000
S×T	3	0.0089
D×S×T	6	0.0138
Error	694	

Analysis 4 (catches over a 3-h period)

Source of variation	D.F.	Tail probability
Depth (D)	2	0.0000
Time (diel period) (T)	7	0.0687
D×T	14	0.0000
Error	456	

Yates (1968) found. Catches and catch rates from different depth strata were dependent on diel period. Catch rates in 91 m were highest during daytime hours while catch rates in 55 and 27 m were highest during nighttime hours (Fig. 4).

Analysis of variance of length frequency samples by depth found that mean sizes of animals were significantly ($P < 0.05$) different between different depth strata (Table 3). The largest mean size of animals were found in 27 m and mean size of animals progressively decreased with increasing depth (Table 4).

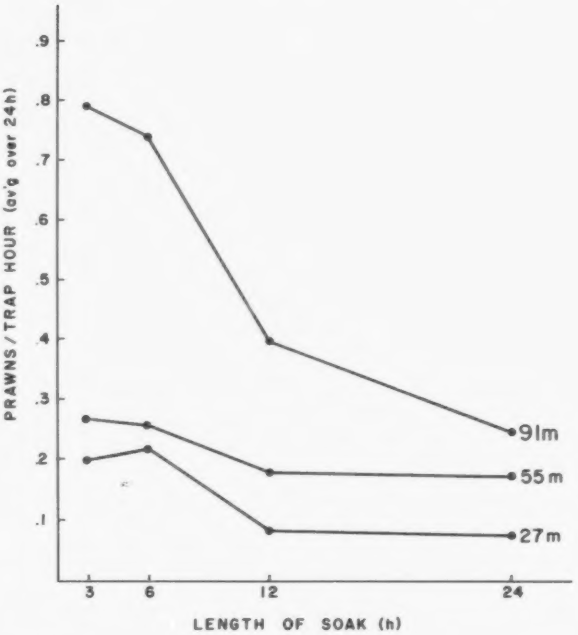

FIG. 3. The average catch rate of prawns for each soak schedule (3, 6, 12, and 24 h) by depth strata.

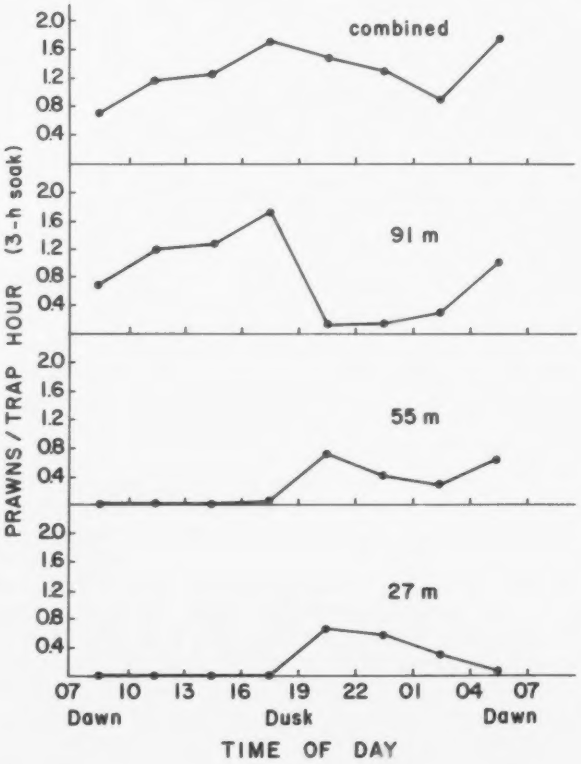

FIG. 4. The average catch rate for 3-h soak schedule over 24 h by individual depth strata and for all depth strata combined.

TABLE 3. Results of the analysis of variance for the length frequency data by depth strata.

Source of variation	D.F.	Tail probability
Depth	2	0.0000
Error	1440	

TABLE 4. Results of ageing analysis of the length frequency data, sample size and percent composition by age for the different depth strata, and the mean size of animals caught at each depth strata.

Age		6 mo	18 mo	30 mo	42 mo
Carapace length		13.2	25.2	34.9	44.3
Depth (m)					
27 Total sample #	264				
#		1	31	111	121
%		.4	11.7	42.0	45.8
Mean carapace size (00.0 mm)	37.9				
55 Total sample #	368				
#		5	44	202	117
%		1.4	12.0	54.9	31.8
Mean carapace size (00.0 mm)	36.8				
91 Total sample #	811				
#		1	53	658	99
%		.1	6.5	81.1	12.2
Mean carapace size (00.0 mm)	35.4				

Discussion

Variations in catches between depth strata may have been caused by animals showing a preferred depth habitat. Berkley (1930), Barr (1967), and Butler (1970, 1980) all observed that juvenile prawns occupy shallower water habitats and emigrate to deeper water habitats a year after hatching. Catches in this study consisted of 99.5% of 1+ aged prawns (Table 4) and the highest catch rates were from the 91 m depth range. The findings would tend to agree that these older prawns are showing the preference for a deep water habitat.

Significant variations in catches seen between different soak times may be caused by a combination of escapement and ingress. Munro (1974) studied the effects of varying soak times on both baited and unbaited traps. He found that in unbaited traps ingress was fairly constant but escapement increased with time until escapement offset ingress and the catch reached an asymptote. In baited traps, he observed that ingress was enhanced and the catch increased until the bait was used up, at this point ingress decreased and escapement increased until the total catch levelled off. The same trends using baited traps were observed in this study. Catch rate was highest for the short 3 and 6 h soaks and decreased significantly for longer soak schedules as the bait was used up (Fig. 3). All the soak schedules were sufficiently long in duration to allow for maximum ingress. Only the 27 m depth strata showed any improvement in catch rate by extending the soak schedule from 3 to 6 h.

Significant variations in catches with respect to diel period were probably caused by a changing diel behavioral pattern. Changes in the diel behavior of pandalid shrimp have been noted previously in a number of studies. Milburn's (1968) and Barr's (1970) trapping studies found nocturnal upward vertical migration for *P. jordani* and *P. borealis* respectively. Barr (1967) made diving observations where juvenile prawns were found inactive and hidden during the daylight hours but actively foraging on the open bottom at night. Chew (1974) conducted a 24-h trawling survey where nocturnal migration of adult prawns into shallow water was suggested.

It is interesting that the mean size of prawns was significantly larger in shallow sets and progressively decreased with increasing depth (Tables 3 and 4). Since the catch in 27 and 55 m sets appear to be prawns migrating into the area at night (Fig. 4) it can be speculated that the larger the prawn the more capable it is to migrate further from its deep water shelter habitat.

Since diel period seems to be important in prawn behavior, it is interesting that it was not significant in the fourth analysis. Figure 3, section D, shows that the 3-h intervals catch rates, for all depth strata combined, do not vary greatly over the 24-h diel period. The reason for this was that daytime catches from 91 m balance the nighttime catches from 27 and 55 m masking the changes in diel behavior.

IMPLICATIONS

This study found that catch rates for the prawn trap fishery vary significantly with depth, soak-time and diel period. At present, catch and effort data analysis appears to be the only logistically feasible method for obtaining abundance estimates in British Columbia's prawn trap fishery.

In stock assessment analysis, large variations in catch rates (Fig. 3,4), will occur when effort standardization does not consider depth, soak schedules or the diel period/depth interaction. These variations caused by unstandardized effort would be confounded with any changes in abundance of prawn stocks and may give misleading conclusions to any stock assessment analysis. In order to bring such a technique on line, further work is required on the definition of effective fishing effort, the technique must be tested against independent estimation techniques and a logbook and biological sampling program must be instituted.

In developing a fishing strategy to maximize profits, the fisherman must weigh funds obtained from total catch against costs (such as wages for crew, costs of bait, fuel costs etc.) associated with various fishing strategies. Tables 5 and 6 indicated the effects on total catch of a variety of possible fishing strategies.

If a vessel is only capable of hauling 40 traps per day (Table 5), then the maximum catch is obtained when 40 traps are set in the 91 m depth strata using a 24-h soak schedule. Total daily catch in this case is 2.2 times that obtained when 5 traps are set at optimum depths and hauled every 3 h. If the vessel can only carry 40 traps, but can haul them on any soak schedule (Table 6), then for a single soak schedule the maximum

TABLE 5. Results of fishing strategies in which the total number of traps that can be hauled in a day is set at 40. The number of traps on inventory varies according to the soak schedule used.

Strategy	Trap inventory	Depth (m)	Soak schedule	Traps hauled per day	Diel period	Total daily catch
A	40	91	24	40	—	242.4
B	40	55	24	40	—	169.0
C	40	27	24	40	—	72.0
D	20	91	12		07:00–19:00	140.6
	20	55	12		19:00–07:00	83.2
				40		223.8
E	10	91	6		07:00–13:00	69.9
	10	91	6		13:00–19:00	46.1
	10	27	6		19:00–01:00	30.9
	10	91	6		01:00–07:00	43.7
				40		190.6
F	5	91	3		07:00–10:00	10.7
	5	91	3		10:00–13:00	17.7
	5	91	3		13:00–16:00	18.7
	5	91	3		16:00–19:00	25.7
	5	55	3		19:00–22:00	11.2
	5	27	3		22:00–01:00	8.9
	5	91	3		01:00–04:00	5.5
	5	91	3		04:00–07:00	12.5
				40		110.9

catch is obtained when the 40 traps are set in optimum depths using a 3-h soak schedule. Total daily catch in this case is 3.7 times larger than that obtained by running 40 traps in the 91 m depth strata using a 24-h soak schedule. The seventh strategy shown in Table 6, is a combination of soak schedules which when compared to the 3 hour soak schedule strategy, uses 75% of the effort and yields an increase of 1.1 times the total daily catch. Austin (1977) points out that profit maximization is not static and will change as abundance of the animals changes. What is important though, is that the model be capable of evaluating relative fishing power of various fishing strategies.

Acknowledgments

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TABLE 6. Results of fishing strategies in which the inventory of traps is fixed at 40. The number of times these traps are hauled varies according to the soak schedule.

Strategy	Trap inventory	Depth (m)	Soak schedule	Traps hauled per day	Diel period	Total daily catch
A	40	91	24	40	—	242.4
B	40	55	24	40	—	169.0
C	40	27	24	40	—	72.0
D	40	91	12		07:00–19:00	281.3
	40	55	12		19:00–07:00	166.3
				80		447.6
E	40	91	6		07:00–13:00	279.7
	40	91	6		13:00–19:00	184.6
	40	27	6		19:00–01:00	123.6
	40	91	6		01:00–07:00	174.6
				160		762.5
F	40	91	3		07:00–10:00	85.8
	40	91	3		10:00–13:00	141.7
	40	91	3		13:00–16:00	149.9
	40	91	3		16:00–19:00	206.0
	40	55	3		19:00–22:00	89.9
	40	27	3		22:00–01:00	71.2
	40	91	3		01:00–04:00	44.2
	40	91	3		04:00–07:00	99.8
				320		888.5
G	40	91	6		07:00–13:00	279.7
	40	91	3		13:00–16:00	149.9
	40	91	3		16:00–19:00	206.0
	40	55	3		19:00–22:00	89.9
	40	27	3		22:00–01:00	71.2
	40	91	6		01:00–07:00	174.6
				240		971.3

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Assessment and Population Dynamics of Commercially Exploited Shellfish in England and Wales

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Fisheries for shellfish in England and Wales are based on a diversity of crustacean and mollusc species, and the present approach to stock assessment is illustrated by reference to problems arising recently in four species. For the lobster, (*Homarus gammarus* L.) size composition analysis, yield per recruit modelling, and limited historical data can be used to describe the present status of eight coastal fisheries. The assessment points to future needs with respect to basic data and field studies of behaviour and pre-recruit ecology. For the scallop (*Pecten maximus* L.) the paper describes the simple application of yield per recruit theory but looks ahead to a proper consideration of the role of spatial dynamics. For the mussel (*Mytilus edulis* L.) and oyster (*Ostrea edulis* L.) historical data are used to show that for some bivalve populations the problem is less one of stock assessment than that of understanding the biology of recruitment.

On pêche en Angleterre et au pays de Galles diverses espèces de mollusques et de crustacés. L'approche actuellement utilisée pour évaluer les stocks est décrite en faisant référence aux problèmes rencontrés récemment chez quatre espèces. En ce qui concerne le homard (*Homarus gammarus* L.), on peut se servir de l'analyse de la composition par taille, de la modélisation du rendement par recrue et d'un nombre limité de données antérieures pour décrire la situation actuelle de huit pêches côtières. L'évaluation fait ressortir les futurs besoins en ce qui concerne les données de base et les études sur le terrain concernant le comportement et l'écologie des pré-recrues. Pour ce qui est des pétoncles (*Pecten maximus* L.), le texte décrit l'application simple de la théorie du rendement par recrue mais va plus loin en faisant un examen approprié du rôle de la dynamique spatiale. Pour la moule (*Mytilus edulis* L.) et l'huître (*Ostrea edulis* L.), on se sert de données antérieures pour montrer que dans le cas de certaines populations de bivalves, le problème consiste moins à évaluer les stocks qu'à comprendre la biologie du recrutement.

Introduction

Shellfish landings in England and Wales are presently worth about £15 million sterling ($Can. 20.3 million) at first sale, equivalent to nearly 20% of the value of demersal fish landed, and nearly twice the value of pelagic fish landed. The industry is based on a diversity of crustacean and molluscan species (Table 1). Four of these have featured in recent stock assessments which illustrate the basis of current shellfish stock management practice at Lowestoft. Analysis is heavily constrained by the fact that relatively few shellfish fisheries have been sampled intensively on a regular long term basis.

Lobster

The European lobster, *Homarus gammarus* (L.) is a prestige species with a high market value, occurring on stony and rocky substrate around the British Isles, principally within 20 km (12 miles) but occasionally further offshore. In 1966 legislation banning the landing of berried females was repealed and fisheries have been managed by minimum size regulation only, except in the coastal area of Norfolk where a local bylaw banning landing of berried females remains. Until recently minimum size was 80 mm carapace length (CL), but recommendations for an increase in minimum landing size (MCL) from 80 to 85 mm CL (Anon, 1978, 1979) have now been implemented (from 80 to 83 mm in May 1981, and from 83 to 85 mm in May 1984). The management position has now been reviewed from a wider standpoint, by modelling the response of yield per recruit and biomass per recruit to changes in minimum size and fishing mortality.

DATA

The main coastal lobster fisheries in England and Wales are found in eight districts illustrated in Fig. 1a. There is no information on whether or not the eight fishery districts correspond to biological stock units. Off the coasts of Yorkshire, Cornwall (Hepper 1978) and North Wales (Simpson 1961), however, tagged lobsters move no more than a few kilometres in a season, and adult interchange between districts is probably unlikely. Districts are therefore used as the unit stock for assessment purposes.

For each district annual lobster size composition data have been obtained regularly since 1972, based on coastal sampling during the main lobster fishing season. For each fishery, sample length distributions (cara-

TABLE 1. Value, landings and unit value of England and Wales shellfish in 1982 (Ministry of Agriculture, Fisheries and Food, Sea Fisheries Statistical Tables)

Species	Value (10^{-3}£)	Landings (tonnes)	Unit value (£ per tonne)
Crab (*Cancer pagurus* (L.))	3231	5404	598
Nephrops (*Nephrops norvegicus* (L.))	3562	3347	1064
Lobster (*Homarus gammarus* (L.))	2103	402	5231
Shrimp (*Crangon crangon* (L.))	822	1202	684
Scallop (*Pecten maximus* (L.))	1623	2343	691
Oyster (*Ostrea edulis* (L.))	925	417	2218
Queen (*Chlamys opercularis* (L.))	463	2094	221
Mussel (*Mytilus edulis* (L.))	453	4388	216
Cockle (*Cerastoderma edule* (L.))	458	8300	55
Whelk (*Buccinum undatum* (L.))	380	1642	231
Clam (*Mercenaria mercenaria*)	104	599	174

£ = pound sterling.

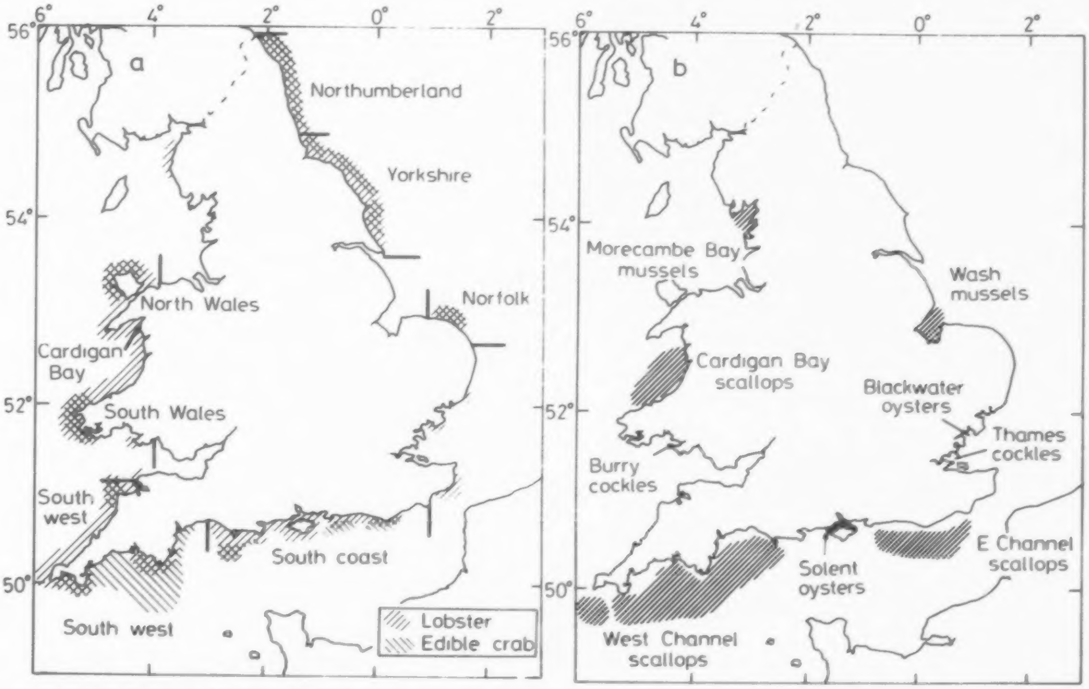
6°
4°
2°
0°
2°
56°
54°
52°
50°
a
Northumberland
Yorkshire
Norfolk
North Wales
Cardigan Bay
South Wales
South west
South coast
South west
▨ Lobster
▧ Edible crab
b
Morecambe Bay mussels
Wash mussels
Cardigan Bay scallops
Blackwater oysters
Thames cockles
Burry cockles
E Channel scallops
Solent oysters
West Channel scallops

FIG. 1. England and Wales shellfisheries. Location of main fisheries discussed in text. a. Crustacea, b. Molluscs.

pace length) have been aggregated within ports on a seasonal basis, before aggregating between ports and raising to the total estimated catch for each fishery. Measurements were grouped in 5 mm length groups, the sexes being treated separately. No discarding correction is necessary since all lobsters above minimum size are landed. Raised data were averaged for the period 1972 to 1980, since data for 1981 to 1984 are not yet in equilibrium with recent changes in carapace length. In the raising procedure weight of each sample is based on a length weight conversion. Length weight relationships, and growth data required for use in length analysis, were kindly made available by D. Bennett, Lowestoft, from his unpublished material, and were presented as Table 2 in Bannister et al. (1983). Von Bertalanffy parameters were derived from Ford-Walford lines fitted to predetermined values of L_∞, and to anniversary growth increments derived from tagging data. They range as follows:

1972–80 All fishery areas, excluding Norfolk.

Male K = 0.09–0.12; L_∞ = 175–210 mm CL.
Female K = 0.07–0.11; L_∞ = 169–200 mm CL.
Norfolk
Male K = 0.24; L_∞ = 150 mm CL.
Female K = 0.21; L_∞ = 150 mm CL.

These compare with values in the range K = 0.11–0.31, L_∞ = 121–197 mm CL from studies by Hepper (1978) for Cornwall, Yorkshire and Wales in the 1960's, and Shelton et al. (1978) for S.E. Scotland.

METHODS

Size composition data for each fishery have been analysed by the Jones length cohort analysis model (Jones 1981) to obtain curves of yield per recruit and biomass per recruit against proportional changes in fishing mortality for a range of minimum carapace lengths from 80 to 110 mm, and two assumed natural mortality values ($M = 0.1$, and $M = 0.2$). In this context the term "per recruit" refers to the number of lobsters occurring in the 80–84 mm length group. Of the two options for natural mortality, $M = 0.1$ is that adopted in Anon. (1979) whilst $M = 0.2$ corresponds to an estimate derived for the Yorkshire area by Hepper (1978). In the 1960's Hepper measured total mortality, Z, from size composition data, and fishing mortality, F, from tagging, and hence estimated M as Z minus F. For the present range of growth parameters a value of $M = 0.1$ will give an M/K ratio close to unity for all fisheries except Norfolk, and a value of $M = 0.2$ will give an M/K ratio of unity for Norfolk but values greater than unity elsewhere. Low values of M correspond to the view that a heavily armoured refuge seeking animal may have few predators.

For descriptive purposes it is helpful to represent the vector of fishing mortality at length as a single value. For the 10 main size classes between 80 and 129 mm CL the options are to calculate the mean of individual values, or a mean weighted either by population number or catch number as suggested by Bannister and Addison (1984), taking an approach analogous to that proposed by Shepherd (1983) for catch at age data. Thus population weighted fishing mortality, F_p, and catch weighted fishing mortality, F_c, are

$$F_p = \frac{\Sigma(P_i F_i \Delta t_i)}{\Sigma(P_i \Delta t_i)} \qquad F_c = \frac{\Sigma(C_i F_i \Delta t_i)}{\Sigma(C_i \Delta t_i)}$$

TABLE 2. England and Wales lobsters. Sample data showing cohort analysis estimates of F at length for different values of terminal F. Northumberland, males, 1978–80, $M = 0.1$.

Length group (mm)	Fishing mortality		
	Terminal F		
	0.4	0.8	1.2
80	0.72	0.72	0.72
85	1.11	1.11	1.11
90	1.14	1.14	1.14
95	0.79	0.79	0.79
100	0.90	0.91	0.91
105	0.60	0.61	0.61
110	0.79	0.80	0.80
115	0.53	0.54	0.54
120	0.45	0.45	0.45
125	0.62	0.64	0.64
130	0.36	0.38	0.38
135	0.42	0.44	0.45
140	0.87	0.94	0.96
145	0.40	0.80	1.20

For length group i, the terms P_i, C_i, F_i and Δt_i are respectively population number, catch number, fishing mortality, and the time taken to grow through the length interval. F_p places more emphasis on smaller size classes, particularly those above the minimum size which are not fully exploited, whereas with F_c most of the weighting is due to modal size classes in the catch, whatever the minimum size.

The Jones length cohort analysis has been adopted because it facilitates yield per recruit analysis by running the model for various proportional increases or decreases in fishing mortality. Mortality alone can also be estimated simply from length compositions using the mean length method of Beverton and Holt (1956), and a length catch curve method described in Pauly (1983). The Beverton and Holt method estimates Z from mean length ($\bar{\ell}$) and the selection length (ℓ_c) as $Z = K(L_\infty - \bar{\ell})/(\bar{\ell} - \ell_c)$, and the Pauly method estimates Z as $\ell n\ N/\Delta t$ against mean relative age for each length group. In both cases Δt is the time taken to grow from one length group to another.

FISHING MORTALITY (F)

For these fisheries F estimates derived by cohort analysis are virtually independent of the assumption about terminal F (e.g. Table 2) and are similar to those obtained by the Beverton and Holt and catch curve methods (Table 3).

Variation between districts and across years is shown in Table 4 using data for 1972–81 grouped as a series of 3-yr running means. F varies both within and between districts. ANOVAR techniques cannot be applied here because the "yearly" data are not independent, but the variation between districts is clearly greater. Table 5 shows that the two weighted estimates, F_p and F_c, were similar because during 1972–80 most of the available size range was exploited in a uniform manner.

Fishing mortality differs considerably between fisheries, with F being highest for fisheries on the east coast and in the eastern English Channel and lower for fisheries on the west coast, in South Wales and the southwest, reflecting differences in size composition between fisheries (shown in Table 1 of Bannister et al. 1983). Unfortunately such differences cannot be associated with fishing effort differences because of lack of data. It has been suggested, however, that the Norfolk size composition, which is restricted primarily to small lobsters, is also influenced by the nature of available substrate (Howard 1980; Howard and Nunny 1983).

F is slightly higher for males than for females probably because of differences in growth rate and because the breeding season leads to a period of reduced female catchability.

For $M = 0.1$ or 0.2 estimates of total mortality, Z, derived from the F estimates obtained here are generally markedly lower than those recorded for the eastern United States, where in Maine, Z averaged 2.2 in the period 1967–70 (Anthony 1980), and in the Canadian Maritimes, Z varied from 0.5 to 3.5 depending on area and year (Campbell 1980).

TABLE 3. England and Wales lobsters. Estimates of the coefficient of fishing mortality for mean 1978-80 size composition using different methods.

Fishery		Jones Method[a]	Beverton and Holt Method[b]	Catch Curve Method[b]
Northumberland	Male	0.74	0.86	—
	Female	0.65	0.69	
Yorkshire	Male	0.70	0.80	0.81
	Female	0.50	0.60	0.66
Norfolk	Male	1.79	1.65	1.80
	Female	1.72	1.65	1.96
South Coast	Male	0.53	0.87	—
	Female	0.45	0.69	
South West	Male	0.39	0.36	0.46
	Female	0.28	0.34	0.26
South Wales	Male	0.36	0.31	—
	Female	0.19	0.15	
Cardigan Bay	Male	0.61	0.74	—
	Female	0.46	0.58	
North Wales	Male	0.74	0.59	—
	Female	0.50	0.51	

[a] Stated value represents mean of first 10 length groups.

[b] F estimated as $Z - 0.1$.

TABLE 4. England and Wales lobsters. Trend in mean[a] fishing mortality, 1972-81.

Period	Fishery								Fishery code
	1	2	3	4	5	6	7	8	
Male									
1972-74	—	0.96	1.99	—	0.30	0.46	0.47	0.68	1 Northumberland
1973-75	0.92	0.93	1.69	0.68	0.27	0.42	0.44	0.62	2 Yorkshire
1974-76	0.78	0.90	1.88	0.75	0.35	0.43	0.46	0.59	3 Norfolk
1975-77	0.77	0.85	1.67	0.68	0.35	0.40	0.48	0.57	4 South Coast
1976-78	0.82	0.78	1.57	0.67	0.46	0.39	0.61	0.59	5 South West
1977-79	0.85	0.76	1.47	0.68	0.33	0.36	0.79	0.84	6 South Wales
1978-80	0.79	0.76	1.68	0.58	0.35	0.34	0.69	0.80	7 Cardigan Bay
1979-81	0.70	0.80	2.07	0.54	0.41	0.24	0.48	0.69	8 North Wales
Female									
1972-74	—	0.77	1.45	—	0.19	0.29	0.41	0.52	
1973-75	0.67	0.81	1.50	0.54	0.16	0.27	0.39	0.49	
1974-76	0.60	0.86	1.86	0.59	0.18	0.22	0.45	0.45	
1975-77	0.60	0.97	1.95	0.57	0.19	0.25	0.43	0.44	
1976-78	0.61	0.67	2.07	0.58	0.20	0.23	0.46	0.40	
1977-79	0.64	0.59	1.72	0.59	0.23	0.23	0.48	0.48	
1978-80	0.67	0.52	1.84	0.48	0.25	0.18	0.51	0.47	
1979-81	0.67	0.53	2.04	0.41	0.31	0.11	0.42	0.45	

[a] Straight mean of length groups 80-129 mm.

YIELD PER RECRUIT VARYING WITH FISHING MORTALITY

Figure 2a illustrates the theoretical curves of yield per recruit (Y/R) and stock biomass per recruit (B/R) for proportional changes in fishing mortality, for $M = 0.1$. Results are shown for three representative fisheries, Yorkshire, Norfolk, and the southwest, where different combinations of growth rate, fishing mortality and size composition create slightly different shapes of yield per recruit curves. Figure 2a predicts that maximum sustainable Y/R will occur at a lower value of F than at present, and for all eight coastal fisheries Table 6, column a, shows the ratio between F at the maximum on the Y/R curve, and present effort. For $M = 0.1$ max-

TABLE 5. England and Wales lobsters. Values of population weighted (F_p) and catch weighted (F_c) fishing mortality for period 1972–80 for size range 80–129 mm. $M = 0.1$.

Fishery	Fishing mortality	
	Population weighted (F_p)	Catch weighted (F_c)
Northumberland		
Male	0.85	0.87
Female	0.66	0.67
Yorkshire		
Male	0.84	0.85
Female	0.72	0.74
Norfolk[a]		
Male	1.65	1.68
Female	1.55	1.59
South coast		
Male	0.83	0.89
Female	0.65	0.67
South west		
Male	0.34	0.36
Female	0.21	0.23
South Wales		
Male	0.39	0.41
Female	0.23	0.24
Cardigan Bay		
Male	0.60	0.63
Female	0.55	0.57
North Wales		
Male	0.64	0.66
Female	0.55	0.56

[a] Size range 80–104 mm only available.

imum sustainable yield per recruit should be obtained at between 0.25 and 0.65 of present *F*, depending on the fishery. If effort was reduced accordingly the *B/R* curves show that stock would be expected to increase substantially.

Figure 2b shows the corresponding result for $M = 0.2$. As would be expected the *Y/R* curves either become more flat topped (in which case reducing *F* generates a much smaller gain in *Y/R*, but still increases *B/R* substantially) or even asymptotic in shape, in which case maximum *Y/R* is predicted to occur at a higher *F* than at present, but with a lower *B/R*. Table 6, column b, shows the corresponding proportional change in *F* required to maximise *Y/R*.

THE EFFECT OF VARYING BOTH FISHING MORTALITY AND SIZE AT FIRST CAPTURE

For the same three fisheries results of varying both *F* and size at first capture are shown in Fig. 3a and b, for $M = 0.1$. Results are similar to those found for other lobster fisheries (Fogarty 1980; Shelton et al. 1978). Either reducing *F* or increasing minimum carapace length (MCL) both predict equilibrium gains in *Y/R* and *B/R* but in general proportional gains in *B/R* are substantially greater than gains in *Y/R*. The relative merit of changing *F* or MCL depends on the interplay between the shape of the yield curve and the level of current *F*, both dependent on the present size composition. For example in Yorkshire both options predict similar gains in *Y/R* but reducing F predicts the best gain in *B/R*. In the other fisheries highest gains in *Y/R* and *B/R* should result from raising MCL. Results for $M = 0.2$ (not illustrated) predict that reducing F or increasing MCL should still produce gains in *B/R*, but because of the change in shape of the yield per recruit curve, already noted, gains in *Y/R* will be reduced (for change in MCL) or eliminated (for changing *F*). Consequences of any particular change in *F* and MCL are not the same for all fisheries. Regionally different regulations would therefore be required to do the best for each fishery.

TABLE 6. England and Wales lobsters. Effort required to obtain maximum sustainable yield per recruit, as a proportion of present effort at two levels of natural mortality (*M*).

Fishery	(a) $M = 0.1$		(b) $M = 0.2$	
	Male	Female	Male	Female
Northumberland	0.40	0.50	0.60	1.15
Yorkshire	0.25	0.40	0.40	1.20
Norfolk	0.60	0.55	0.75	0.65
South coast	0.45	0.45	1.10	1.30
South west	0.65	0.65	1.80	>2.0
South Wales	0.45	0.55	1.10	>2.0
Cardigan Bay	0.40	0.40	1.50	1.95
North Wales	0.25	0.35	0.70	1.20

The Jones model reaches equilibrium by a series of annual iterations which show the time path of losses and gains. In the main the immediate loss phase for a change in carapace length is about 2 yr at current growth rates whilst full gains require 4 or more years to materialise (Bannister et al. 1983). Size composition data have not yet been tested for results of the present MCL changes.

CONCLUSIONS FROM YIELD PER RECRUIT

Results for $M = 0.1$ show that, with present *F* values, changing MCL is only one management option for lobsters, and that for some fisheries reducing effort substantially could maximise *Y/R* and produce marked gains in *B/R*. On the other hand, if $M = 0.2$ the benefit to *Y/R* of further increases in MCL, or of a decrease in effort, will largely be eliminated and only gains in *B/R* will remain. Conversely, if $M = 0.2$ and *F* is increased there could be an increase in *Y/R*. Consequently where the management objective is to maximise *Y/R*, *F* would have to increase or decrease according to the assumption about *M*. This ambiguity does not arise if the objective is to increase *B/R*.

BERRIED FEMALES

In some areas, notably Yorkshire, English fishermen say they would prefer legislation which bans the landing of berried females to changes in MCL. This was dis-

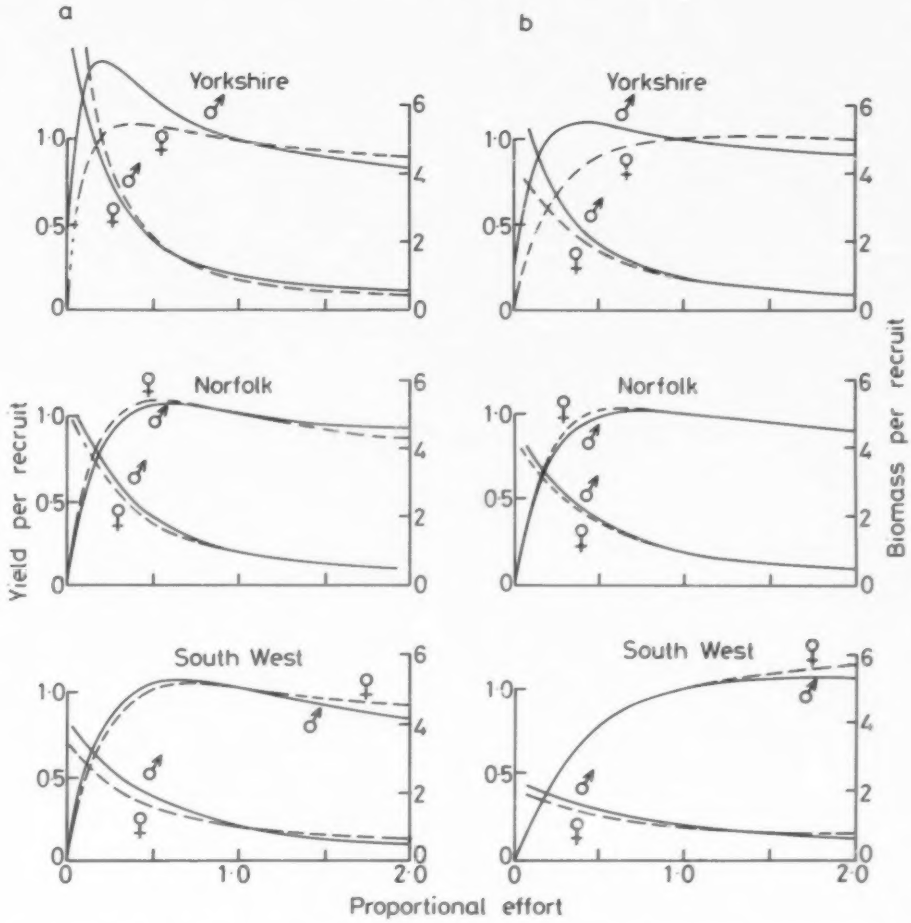

FIG. 2. England and Wales. Three lobster fisheries. Proportional change in yield per recruit and stock biomass per recruit against effort, relative to 1978–80 values. a. $M = 0.1$, b. $M = 0.2$. Full line = male. Broken line = female.

cussed by Bennett and Edwards (1981), who predicted that substantial gains in egg production per recruit would follow from changing either MCL, or introducing a berried female prohibition. The berried female legislation could produce greater gains in eggs per recruit, but it would also produce immediate losses in yield which would not result in long-term gains in all areas. Further, an increase in egg production does not necessarily lead to an increase in recruitment. Bennett and Edwards therefore favoured the all round benefits of changing MCL because the smaller gains in egg production per recruit would be balanced by long-term gains in Y/R in all areas. A minimum size regulation is also easier to enforce. This view is in contrast to that which obtains in eastern USA and Canada, where a ban on taking berried females supplements the minimum size legislation.

HISTORICAL TRENDS

Historical data for these fisheries are limited. There is some evidence for Yorkshire and Cornwall, however, that fishing mortality has been maintained at approximately present levels for most of the century. Hepper (1978) illustrated mean size compositions for several historical periods, 1907–08, 1938–39, 1956–60, 1959–68. Using the cohort analysis method rough estimates of F obtained from published histograms are in the range

	Male	Female
Yorkshire	0.6–1.1	0.4–0.7
Cornwall	0.4–0.6	0.3–0.5

which is similar to the 1972–80 estimates.

For Yorkshire an estimate of the aggregate catch per unit effort (CPUE) for the main ports from 1966 to 1975 (Fig. 4a) can be used to estimate total effort as the quotient of total catch and CPUE (Fig. 4b). The data are uncorrected for a change in the fishing power of the traps occurring when creels were replaced by parlour pots in the 1960's. Unexpectedly both show a prolonged decline. Following an equilibrium in F suggested by historical size distribution data one might expect that a decline in effort would lead to an increase in CPUE. The fall in CPUE does not seem to be in doubt because individual fishermen's log books show trends similar to the aggregate index. Although individual catch and effort, and hence CPUE, have been reported correctly, it is possible that census of total catch has been incom-

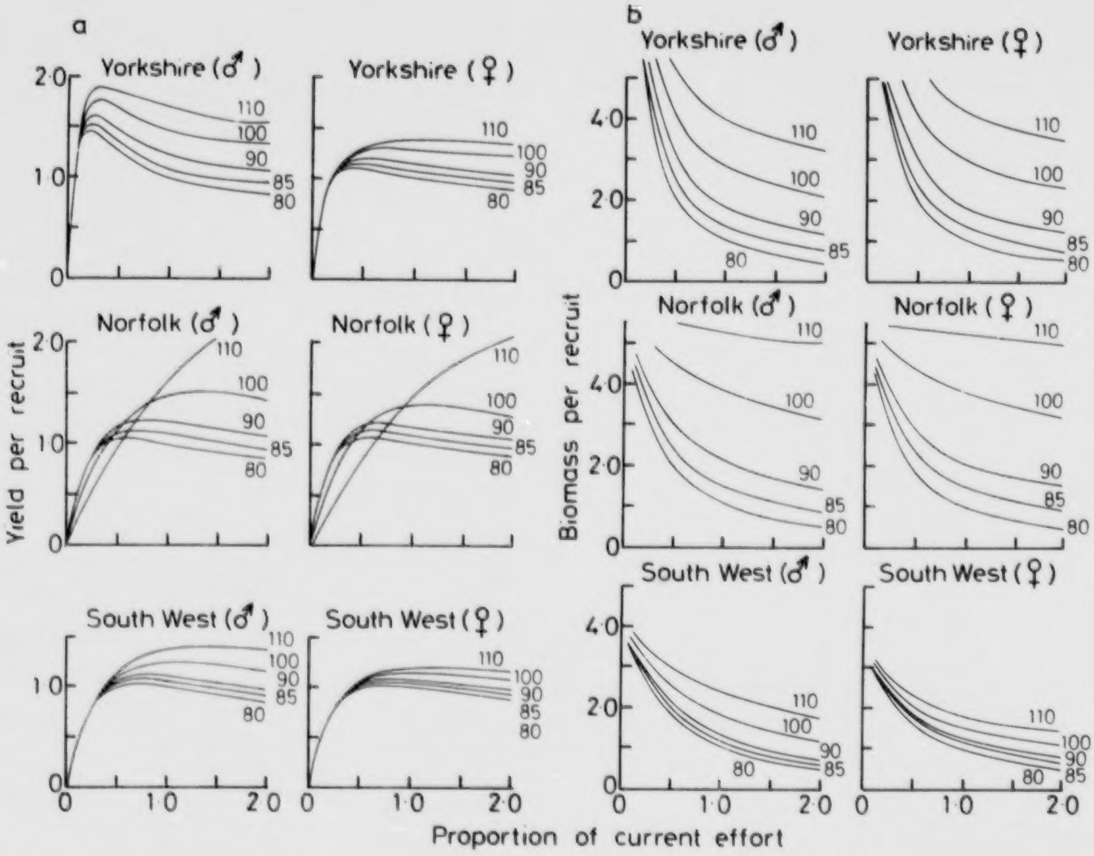

FIG. 3. England and Wales. Three lobster fisheries. Proportional change in yield per recruit and stock biomass per recruit against effort, for different carapace lengths, relative to 1978–80 values. $M = 0.1$. a. yield per recruit, b. stock biomass per recruit.

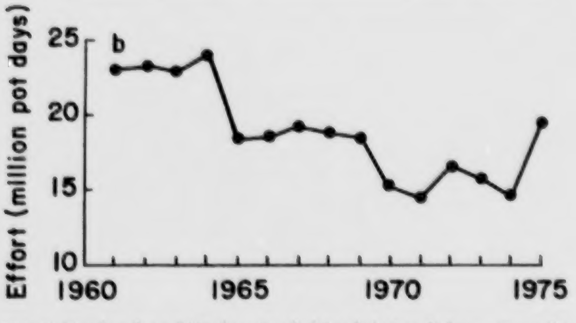

FIG. 4. England and Wales. Yorkshire lobster fishery. Trend in a. catch per unit effort (CPUE) and b. total derived effort. 1961–1975.

plete, hence underestimating derived effort. A more probable explanation however is that decline in CPUE has caused effort to switch away from lobster fishing, since, in the 1960's, trawling became more popular on the east coast, and better prices made the *Cancer pagurus* fishery more attractive. There are no independent data for lobster recruitment, so the hypothesis that decline in CPUE involves a fishery or environmentally related decline in recruitment cannot be tested. A similar concordant decline in effort and CPUE occurs in the adjacent east coast district of Northumberland, and has been described for the Norwegian fishery by Tveite (1979). A decline in CPUE was not universal, however, since data for the Norfolk fishery, south of Yorkshire, are cyclical and without trend.

Since 1972 there has been a downward trend in fishing mortality in Yorkshire and Northumberland (Table 4) but two estimates of Yorkshire trap effort obtained by interview in 1973 and again in 1984 suggest an effort increase of about 20% in this period. This disparity could reflect a further switch away from lobster fishing to crab fishing. The possibility of bias in the mortality estimate, as a result of say a decline in recruitment of young lobsters, cannot be tested independently.

STOCK AND RECRUITMENT

Setting aside the various uncertainties associated with measurement of *F*, the conclusion from the section on Y/R analysis is that, at present, *F* generally exceeds F_{max}. The *Y/R* model predicts that for $M = 0.1$ a reduction in F should give small increases in equilibrium *Y/R* and moderate to substantial increases in *B/R*, but that an increase in *F* will have little effect on either *Y/R* or *B/R*. Unfortunately the risks to recruitment likely to be associated with an increase in *F* cannot be quantified objectively for these fisheries. Anon (1979) and Bennett and Edwards (1981) both expressed concern about the possibility of a lobster recruit failure. The view was, however, intuitive, since data on stock and recruitment were not available. The position on data is unchanged. The present time series of length composition data is short, and in any case estimates of total catch from fisheries are unreliable and throw considerable doubt on the usefulness of estimates of stock biomass and recruitment derived from cohort analysis. It is also difficult to comment objectively about dangers of maintaining or increasing F especially when seen from the viewpoint of fisheries elsewhere. For example lobster fisheries in Atlantic Canada are now considered to suffer from recruitment overfishing (Pringle et al. 1983) yet even quite recently a conclusion on the effect of fishing on recruitment has been a matter of some debate (Dadswell 1979; Robinson 1979). In any case, as noted previously, *F* values in Canadian fisheries have been substantially higher than those in English fisheries for a considerable time.

Despite the foregoing it is clearly advisable for the manager to move away from implicit acceptance of the *Y/R* model. This is not easy to remedy, however. Even if a methodology is developed for collecting systematic and representative stock and recruit data from these fisheries, it will take time to accumulate observations, and there is no certainty that a clear cut trend or relationship will emerge. Consequently in my view the only immediate way forward is by a modelling approach. Shepherd (1982) described a flexible function which facilitates the fitting of families of stock and recruit curves of varying shape by varying the parameter values selected for density independent and density dependent terms. Curves are fitted to typical observations on biomass and recruitment, and the function can be transformed to obtain curves of true yield and biomass against *F* using *Y/R* and *B/R* data. In principle this method can be adapted to a simulation study of the effect of different assumptions about the shape of the stock-recruit curve. If we assume that the limited output from the 1972–81 length cohort analysis provides typical mean values of biomass and recruitment for scaling purposes only, then various shapes of stock-recruit curves can be fitted through this point using a range of values for the other terms. Their general effect on management options can then be compared. This should at least clarify implications of either obtaining or rejecting the *Y/R* model, and may lead to predictions about the pattern of change of equilibrium yield or biomass to be expected for changes in fishing effort, which could be verified independently using catch or CPUE data. Preliminary results from this approach will be available shortly (Bannister and Addison, unpublished data).

DISCUSSION FOR LOBSTERS

Although size composition and *Y/R* analysis provide a general assessment of the state of English lobster fisheries a number of problems remain to be resolved or investigated. Overall the data base is poor and analysis of long-term trends in catch, effort and CPUE is incomplete. There are corresponding doubts about the validity of cohort analysis estimates of biomass and recruitment. The relation between fishing effort and mortality is at present assumed to be proportional but needs testing since there is considerable uncertainty about how behaviour and distribution of lobsters influence catchability and in particular whether gear interaction limits fishing mortality likely to be generated at high trap densities. The assumption that size composition changes as *F* changes also needs testing in light of observations on the possible effect of substrate limitation on the Norfolk size composition. In fact in terms of current prediction for management the present combination of parameters at Norfolk does not preempt changes predicted there for at least moderate changes in MCL, provided that M is still low for small lobsters and only increases at the higher end of the size range (Table 7). However, it is clearly important to test for this type of problem in other areas. Finally it will also be worthwhile to extend the conventional treatment to consider interaction between lobster and *Cancer pagurus* fisheries, which occur on the same grounds on some coasts. A complication here is that the lobster is relatively sedentary but the crab shows both a female spawning migration and inshore–offshore movement (Bennett and Brown 1983) which will complicate the analysis of size composition data and the relation between fishing effort and mortality.

TABLE 7. England and Wales lobsters. Predicted long-term gains in yield and stock biomass in the Norfolk fishery for different schedules of natural mortality.

Size class (mm)	Size dependent mortality values			
	1	2	3	4
80-4	0.10	0.10	0.10	0.10
85-9	0.10	0.10	0.10	0.10
90-4	0.10	0.10	0.15	0.10
95-9	0.10	0.15	0.15	0.35
100-4	0.10	0.15	0.20	0.35
105-9	0.10	0.15	0.20	0.35
110-4	0.10	0.25	0.30	0.35
115-9	0.10	0.35	0.30	0.35
120-4	0.10	0.45	0.40	0.35
125-9	0.10	0.50	0.40	0.35
130-4	0.10	0.60	0.40	0.35
135-9	0.10	0.60	0.40	0.35
Carapace change 80–85 mm				
% Gains in yield	8.85	8.05	7.54	6.39
Stock biomass	43.58	43.03	42.46	41.42

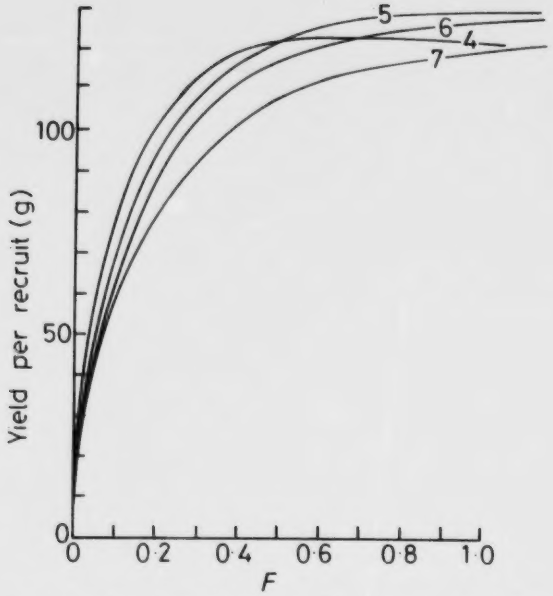

FIG. 5. England and Wales. Cardigan Bay scallop fishery. Curves of yield per recruit against fishing mortality at four ages (yr) of first capture. $M = 0.15$.

Improved European lobster assessment therefore requires not only a greatly improved data base, but a considerable range of studies on ecological, behavioural and fisheries issues.

Scallops

The scallop (*Pecten maximus* L.) is widely distributed in coastal waters out to between 19 and 97 km (12 and 60 miles) and in the eastern and western English Channel and Cardigan Bay (Fig. 1b). Since the early 1970's scallop fishing has become prominent in these areas. Scallops are also fished extensively around the Isle of Man and in Scottish waters, where separate research investigations are in progress (Mason 1983).

STOCK ASSESSMENT

Scallop research by the Ministry of Agriculture, Fisheries and Food has been confined mainly to use of dredge surveys to determine the main areas of distribution and to obtain general data on age distribution and growth. Fisheries have tended to move rapidly from bed to bed within and between areas, so that population data are difficult to collect by port monitoring methods, and there are no long time series.

A typical fishery episode is that for Cardigan Bay, where a short but intensive fishery developed in 1980 and 1981, rapidly depleted the main beds then moved on. Figure 5 shows *Y/R* curves calculated using local growth data and an assumed value of $M = 0.15$, for different ages of first capture. M was estimated from the recapture rate of dead tagged scallops off Plymouth in 1968/69 (A. Franklin, unpublished data). For 1980 Cardigan Bay, F was estimated as 0.3 using the ratio of total catch to an estimate of stock obtained by research vessel survey. This is similar to the value of F estimated for Scottish stocks, where more detailed and regular age sampling facilitates the use of virtual population analysis (Mason et al. 1979b). For ages of first capture of 4 to 6 yr the Y/R curves are asymptotic and absolute $F_{\max}$ is close to $F = 1.0$ at an age of first capture of 5 yr. At $F = 0.3$, maximum Y/R occurs at an age of entry of 4 yr, equivalent to a minimum size of 110 mm length, and is only a few percent below the best Y/R obtainable. 110 mm length is close both to the preferred market size and the 50% point (equivalent to 20% efficiency) on the size-efficiency ogive for spring-loaded dredges (Mason et al. 1979a), and in 1984 it was adopted as a management measure for this fishery together with a July to December closed season. The latter corresponds broadly to the spawning period (Connor 1978) but was in fact accepted by fishermen primarily to protect their fishery when markets are seasonally poor.

POPULATION DYNAMICS

It is notable that except for minimum sizes and closed seasons English scallop fisheries are unregulated. In the past it seems to have been assumed that boom fisheries, attracted by local recruitment peaks, are self-regulating. Thus, in Cardigan Bay, where a fishery at $F = 0.3$ was well placed on the Y/R curve, the top vessels moved on within 2 yr once catch rates became uneconomic. This does not say much for the prospects of local vessels left behind, however, and it ignores the possibility that the crucial variability in recruitment may be spatial not temporal. Regular scallop age compositions, implying that recruitment occurs regularly each year, seem quite common (e.g. Mason et al. 1979a; Briggs 1980). As noted by Gruffydd (1974) for an unfished part of the northern Irish Sea, age data from individual beds were particularly variable, whilst their overall sum produced a smooth catch curve. Recruitment is therefore probably regular in time but, within a population, variable in space (Caddy 1975). Because scallop dredges have a relatively low efficiency it is possible that only the highest scallop densities suffice for economic exploitation, leaving residual stocks which will always be sufficient for replacement, but it is also possible to imagine that particular spatial patterns of larval production and drift hold the key to recruitment. If recruitment is spatially dependent in this way a particular scale of density and aggregation may well be associated with biological stability and this could be threatened by successional depletion by a mobile fishery such that local depletion should be properly managed. The conventional yield per recruit model takes no account of these features and ignores this interpretation of biological possibilities.

With these factors in mind the emphasis of the Lowestoft scallop programme has recently shifted to include a study area approach. The objective is to attempt to understand the relation between the dynamics of patches, and whether a specific stock-recruit response is likely to be associated with spatial questions.

Finally attention should be paid to the assumption about M since the value used in the Cardigan Bay work is different from that implied by the virgin catch curve of Gruffydd (1974). This indicates age specific values of M rising from 0.16 at age 7 to 0.3 at age 13, and to much higher values beyond. Gruffydd (1972) also showed that dredging may cause considerable incidental damage mortality on the beds. Knowledge of the process of depletion from natural and fishery causes seems particularly rudimentary in this species.

Mussels

In England and Wales the mussel (*Mytilus edulis* L.) occurs intertidally in commercial quantities in two main locations, Morecambe Bay on the west coast, and the Wash on the east coast (Fig. 1b). Large mussels are harvested for consumption, and smaller 'seed' mussels from crowded or exposed beds are used for relaying and on-growing.

POPULATION DYNAMICS

Whereas for the scallop the net effect of the various spatial factors is to produce the profile of a regularly renewable resource, the mussel may not conform to such a pattern. It seems to show a pattern of high natural mortality and intermittent recruitment which renders conventional fishery management difficult. For Morecambe Bay, Dare (1976) found that annual mortality could reach 95% as a result of storm action in winter; suffocation from summer biodeposits; and periodic predation by the sea star, *Asterias rubens* (L.). Consequently, Morecambe Bay mussels have an uncertain existence and rarely live beyond three years of age. The source of recruitment is also difficult to determine. Dare (1976) showed that although plantigrades occur abundantly at peak spawning time in mid-summer, the major crop-producing settlements appeared much later in winter and spring when local plantigrade abundance was low. The stock is therefore probably not self supporting but dependent on bysso-pelagic drift from elsewhere, perhaps from as far away as the Irish Sea. Despite the uncertainty mussel production of survivors is high, being of the order of 0.92–3.75 kg of dry flesh per square metre (Dare 1976).

STOCK MANAGEMENT

Such dynamics, coupled with the usual inadequacies of the data base, make mussel stock management particularly difficult. In the Wash fishery, for example, there has hitherto been no regular stock assessment monitoring but advice has recently been called for because stocks are low. Estimates of stock size were made in 1982 and 1983 using a random transect method to measure density and percentage cover for each bed with the following result for seed mussels and adults:

	Quantity (t)	
	Seed	*Adult*
1982	10200 ± 2550	7900 ± 1700
1983	2100 ± 150	4450 ± 315
1982/83 Catch	—	3000

Depletion of large mussels, equivalent to an annual Z of 0.57, was mainly due to harvesting but a substantial depletion of seed mussels potentially available for relaying took place in the 1982/83 winter as a result of natural causes. Present stock is therefore low and will have been depleted further during subsequent winters. The questions are whether stock recovery can be predicted and whether it is in any way dependent on level of stock on the beds. Preliminary indications are that both are unlikely. Firstly, in 1983, spat collectors identified a clear spat production curve in mid-summer, but there was no settlement on the beds, suggesting that as in Morecambe Bay recruitment is probably from an external source. Secondly, since 1895 historical records of local fishery officers have recorded spatfall qualitatively as good, poor etc. When these are transcribed to an arbitrary numerical scale they suggest that recruitment is log normally distributed (Fig. 6a). Most settlements are therefore rather small and large year classes are rare events. Conditions which favour good year classes are not known but they do not seem to be locally stock dependent. For 1921 to 1955 the fishery officer record showed stock size as the acreage of bed covered by mussels. Figure 7a and b illustrates the time trends for two parts of the Wash, indicating long scale fluctuations, seventeen years peak to peak on the north side, and rather more frequently on the south side. Bed areas, combined and scaled numerically, can be related to the spatfall data as in Figure 6b. Although only quasi-quantitative these data do not suggest that large settlements require a build up of large stock, or, alternatively, that large settlements can only occur when stock is low and available space high (compare the spatially density-dependent regulatory mechanism observed by Hancock 1973, for the cockle *Cerastoderma edule* L. in the Burry Inlet in Wales).

The fishery officer index of stock size ceases in 1955. Subsequent stock decline has therefore not been monitored but it could be due to overfishing. Up to 1955, landings (Fig. 7c) varied between one and a few thousand tonnes. They were not obviously stock dependent and suggest that the exploitation rate was rarely in excess of 0.3 (Fig. 7d). (This was calculated using a stock estimate based on the product of bed area and a mean density based on local experience of mussel production; P. J. Dare, personal communication). In the mid and late 1970's, however, landings exceeded 5000 t on three occasions, and reached 9000 t once, in response to a short-term market demand for seed mussels for export and this has probably depleted stock to its present low level. On the other hand, Figure 6b suggests that the occurrence of the next large spatfall may well be quite independent of this low stock level, and that a solution to the present problem depends as much on understanding the biology of recruitment as on attempting to manage the fishery.

Oysters

The final mollusc example is the oyster, *Ostrea edulis* (L.), which supports the specialist English oyster trade. It is difficult to know whether these populations should be modelled at all, for both trade and natural reasons.

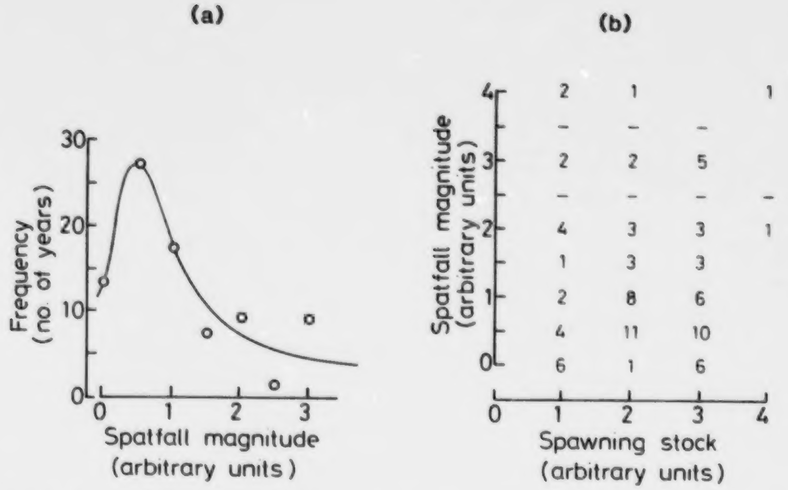

FIG. 6. England and Wales. Wash mussel fishery 1895–1981. a. Frequency distribution of spatfall magnitude. Arbitrary units (see text). Fitted by eye; b. Recruitment on stock historical frequency of scenarios. Arbitrary units (see text).

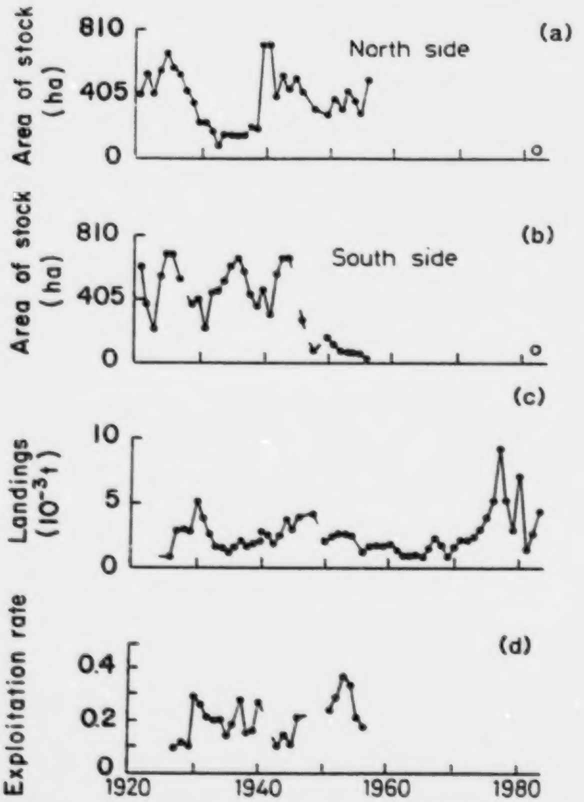

FIG. 7. England and Wales. Wash mussel fishery. Trend in: a,b. Area (ha) of beds, 1921–55. c. Landings (10^{-3} t), 1927–1983 d. Exploitation rate (F), 1927–55. Derived from Annual Reports of the Eastern Sea Fisheries Committee.

Hancock (1973) remarked on the apparent inability of oyster stocks to recover from bad winter losses. This is shown by part of a population in the River Blackwater in Essex on the English east coast. Results of intermittent dredge surveys (Fig. 8) show that the stock was low in the 1950's, built up due to good spatfall in the late 1950's, and then crashed following what was observed at the time to be virtually total mortality in the 1963 cold winter. It has not recovered.

The second example is that of the Solent, on the south coast, which has supported an oyster fishery intermittently in the past. A period of commercial fishing ended in the 1920's but a fishery developed again suddenly in the late 1960's, and built up following good settlements between 1974 and 1978 (Key and Davidson 1981). Since 1978 however there has been little or no settlement, and the large fishery which developed in the meantime has reduced abundance progressively at a rate equivalent to an annual Z of 0.4 (Fig. 8, inset). Trade preference is for 63 mm ring size oysters, which are smaller than the size of 99 mm at which a cohort of oysters would maximize its contribution on the basis of energy considerations. The future of this stock, which is currently the only large source in England of native flat oysters free of the recently introduced protozoan parasite *Bonamia ostreae*, is now in doubt, as also, therefore, is the income of nearly 150 paying licence holders. Conditions favouring settlement in the Solent have not been investigated, and managers face the difficulty that even if the fishery, which is seasonal, could be closed, a recovery of the stock does not necessarily follow. The solution to this problem depends not on fish stock assessment methodology but on acquiring further biological knowledge, and on applying cultivation techniques to bolster existing production.

Discussion

Examples quoted here incorporate a range of different species, modelling and data problems. With adequate basic data, the renewable lobster resources can be assessed by using size distribution analysis, although in light of the possible effect of habitat on size distribution the possibility of bias must be borne in mind.

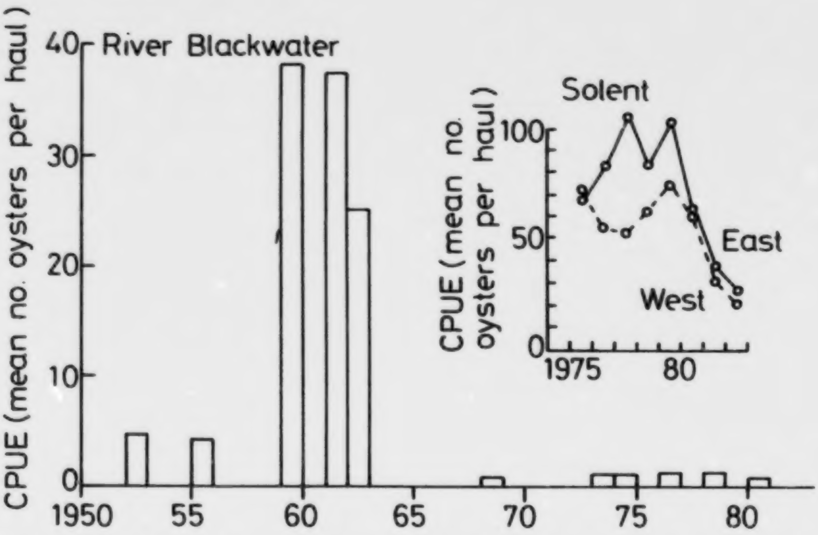

FIG. 8. England and Wales. River Blackwater and Solent oyster fisheries. Trends in mean catch per effort (oysters per haul) in research vessel dredge survey (1 m Baird dredge) for central part of R. Blackwater, and east (solid line) and west (dashed line) Solent. Blackwater data are geometric means for all stations. Solent data are arithmetic means for individual grounds, grouped up for each sector.

For English fisheries the main challenges are to study fundamental distributional, behavioural and regulatory features which determine the shape of the stock-recruit curve, and to investigate the relation between fishing effort and fishing mortality.

The English mollusc fisheries have been much less studied and are a difficult group. There has been little conceptual progress and only nominal stock assessment progress since the report of Hancock (1973). For the scallop it may be that conventional yield models will be verified as representing the sum total of spatial events in a population but this cannot be assumed until the spatial events are fully studied. Present regulations for scallop fisheries probably achieve little and it is possible that when the spatial dimension of stock, fishery depletion and recruitment are understood, control of local depletion may become necessary. Finally mussel and oyster examples show that short-term management decisions are exceedingly difficult to take for populations with a high natural mortality and with a pattern of recruitment which is erratic and whose mechanism is not understood. Fishery models as such are less important than fundamental ecological investigation, but advice based on routine surveys can make a contribution in the short term.

Acknowledgments

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Size, Environment, and Density: The Regulation of a Scallop Stock and its Management Implications

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Orensanz, J. M. 1986. Size, environment, and density: the regulation of a scallop stock and its management implications, p. 195–227. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

The tehuelche scallop (*Chlamys tehuelcha* (d'Orbigny)) stock of the San José Gulf, Argentina, was studied through a combination of intensive (process oriented) sampling of one ground (San Román) and extensive (pattern oriented) surveys of the whole region. The stock is structured as a megapopulation whose components ("grounds") are interconnected by larval dispersal.

The San Román population was regulated by a combination of density-dependent growth, reproductive potential, and recruitment, and size-dependent mortality. Average biomass and annual production were locally constrained by carrying capacity. Year class strength and average biomass showed a 5-yr cycle over the 15-yr period (1969–83) for which information is available. Most individual scallops occur at high densities which makes density-dependent processes important even if they operate over small areas.

Each ground seems to be exposed to a distinct regime of food availability, predation and disturbance. Catastrophic mortality (stranding) and pattern of nitrate consumption by primary producers (phytoplankton and benthic algae *Codium* and *Ulva*) seemed to determine most observed between-grounds differences in shallow, subtidal community structure and scallop population dynamics.

The effects of two alternative harvesting techniques, dredging and commercial diving, are considered and the latter requires less regulation. There is much concern about the deleterious effects of dredging on fishing grounds. A deregulated (but closely monitored) commercial diving fishery and restricted experimental dredging are suggested for future fisheries development.

Le stock de pétoncles *Chlamys tehuelcha* (d'Orbigny) dans le golfe San José, en Argentine, a fait l'objet d'études comportant un échantillonnage détaillé (axé sur les processus) d'un gisement (San Román) et des levés généraux (axés sur les profils) dans toute la région. Le stock a une structure de mégapopulation dont les composantes, ou gisements, sont reliés entre elles par dispersion larvaire.

La population de San Román était régie par une combinaison de facteurs naturels : croissance en fonction de la densité, viabilité, recrutement équilibré et mortalité en fonction de la taille. La capacité de port limitait localement la biomasse moyenne et la production annuelle. D'après les renseignements disponibles qui couvrent une période de 15 ans (de 1969 à 1983), l'effectif des classes annuelles et la biomasse moyenne présentaient un cycle de 5 ans. Puisque la densité de la plupart des zones où l'on trouve des pétoncles est élevée, les processus qui sont fonction de la densité sont très importants même si leur champ d'action est petit.

Chacun des groupes semble être soumis à un régime distinct de disponibilité de nourriture, de prédation et de perturbations. La mortalité catastrophique (échouement) et le profil d'absorption du nitrate par les producteurs primaires (phytoplancton et algues benthiques *Codium* et *Ulva*) semblent être responsables de la plus grande partie des différences observées au niveau de la structure des communautés infratidales en eau peu profonde et de la dynamique des populations de pétoncles.

Les effets de deux méthodes distinctes de capture, le dragage et la plongée commerciale, sont évalués; la plongée commerciale nécessite une moins grande réglementation, alors que les effets nocifs du dragage sur les sites de pêche sont préoccupants. Nous suggérons l'implantation d'une pêche par plongée déréglementée mais étroitement surveillée, ainsi que des dragages expérimentaux limités.

Introduction

Between 1969 and 1971 a fishery for tehuelche scallop (*Chlamys tehuelcha* (d'Orbigny)) developed and collapsed in the northwest part of San Matías Gulf (northern Patagonia, Argentina, Fig. 1b) (Olivier and Capitoli 1980; Orensanz et al. 1985). When new scallop beds were located in the adjacent San José Gulf (Fig. 1b,c), the provincial fishery administration imposed a temporary closure from fear the history of the San Matías fishery would be repeated. Research reported here was undertaken to provide guidelines for exploitation of the San José scallop stock.

The core of this contribution resulted from 3 yr (Nov. 1974 to Nov. 1977) of monthly sampling of the San Román ground (Fig. 1c). It deals with basic aspects of the dynamics of that population (distribution, age, growth, survival, reproduction, recruitment, and production). Simultaneous and concurrent investigations examined environmental factors and primary production (Charpy-Roubaud et al. 1978, 1982, 1983; Charpy et al. 1980a,b,c), scallop feeding (Vernet 1977), scallop reproduction (Lasta and Calvo 1978), and scallop biochemical composition (Pollero et al. 1979). Several surveys between 1973 and 1977 produced data of larger scale patterns of scallop distribution. The reader is referred to Orensanz et al. (1985) for details on methods, summaries of numerical results, and further information on San José Gulf, the tehuelche scallop, and its fishery.

In this paper I present and discuss results concerning the effects of three broad categories of variables, size, environment, and density, on scallop abundance on one ground (San Román), with some between-ground contrasts, and implications for productivity and resource management. An extensive literature exists on size-related biological phenomena in bivalves and on the effects of environmental factors on growth, mortality, recruitment, and distribution. In contrast, density-dependent effects are difficult to establish and remain poorly understood. My results contribute to growing evidence showing that density-dependent processes may be of great importance in the population dynamics of suspension-feeding bivalve populations, even if they occur over relatively small geographical areas.

General Information on the Ecosystem, the Species, and its Fishery

Area Description

San José Gulf (42°14′ to 42°26′S, 64°02′ to 64°36′W; Fig. 1), about 43 by 18 km, is a roughly oval-shaped basin connected to San Matias Gulf through a narrow (9 km), relatively deep (80 m) mouth. The bottom below 35 m is a flat muddy plain. Circulation is driven by tides (range: 2.9 to 8.7 m mean neap and spring tides) and winds (15 km/h average), predominantly from the SW. Water inputs other than those coming from the adjacent ocean are small: there are neither estuaries nor important human settlements; average annual precipitation is 180 mm. Surface water temperature ranges seasonally from 9 to 17°C (Fig. 4a).

The Gulf is at the boundary between the southwestern Atlantic cold and warm temperate biogeographic provinces (Fig. 1a). Benthic fauna and flora reflect this fact (Boschi and Fenucci 1972), being a mixture of components of the two biota: warm temperate species predominate in shallow areas, magellanic elements in the deeper (colder) central basin.

Beds of green algae, *Ulva* and *Codium*, define much of the physiognomy of the shallow subtidal seascape. The first species forms extensive seasonal coverings along the N, NW and SW coasts, becoming scarcer towards the SE corner. There the bottom is characterized by a sparse *Codium* population (Fig. 7b). The shallow subtidal epifauna is dominated by three suspension feeding molluscs: blue mussel (*Mytilus edulis chilensis*), southern mussel (*Aulacomya ater*), and tehuelche scallop.

The spring phytoplankton (resuspended microphytobenthos not discriminated) bloom starts by early October (Fig. 4c,d, and 6 b,c); a second, smaller bloom (late summer/early fall) occurs in late February. Average gross and net annual production was estimated at 223 and 161 $g\,C{\cdot}m^{-2}{\cdot}yr^{-1}$ respectively. Primary production is limited by the availability of nitrates (Charpy-Roubaud et al. 1978, 1983; Charpy et al. 1980a,b,c). Surface and near-bottom samples showed similar seasonal fluctuations (Fig. 4c,d).

Scallop Biology

The tehuelche scallop is a warm-temperature species endemic to the Argentine Biogeographic Province; it inhabits the shallow shelf bottoms from Rio de Janeiro (23°S) to Camarones (45°S) (Fig. 1a). The study area (Fig. 1a,c) is near the southern extremity of its range.

C. tehuelcha is a simultaneous hermaphrodite (Christiansen and Olivier 1971). In the San Román ground there is a partial spawning of both parts of the gonad by late spring; both pre- and post-spawning stages coexist over the summer (Lasta and Calvo 1978). Complete spawning occurs by the end of the summer and is followed by rapid phagocytosis of the residual material; oocyte proliferation occurs over the entire winter. Main annual growth rings (S_i) are laid down in late spring/early summer in the San José Gulf area and are related to spawning; winter rings (W_i) are always weak (Orensanz et al. 1985).

Scallop's diet is mainly benthic microscopic algae, probably resuspended by tide- or wind-generated near-bottom currents or turbulence. Diatom species which live attached to sand grains are rarely found in stomach contents (Vernet 1977).

Fisheries

Scallop fisheries in the San José and San Matias gulfs were very small until the late 1960's, with landings sold exclusively in local markets. By the late 1960's there was a sharp decline in catch per unit effort (CPUE) of scallops on Georges Bank (USA and Canada), which supplied most of the U.S. demand. Following a rise in price for scallop meats in the U.S. market (Caddy and Lord 1971), US dealers searched for new sources of supply. Small scallop fisheries developed or expanded in different areas of the world, among them one for tehuelche scallop in northern Patagonia. Most catches came from dredging grounds in NW San Matías Gulf with landings in San Antonio Oeste (Fig. 1b). The fishery peaked in 1970, when more than 10 000 t were landed (Olivier and Capitoli 1980).

The fishery of San Matias Gulf collapsed suddenly after 3 yr of intensive harvest (Orensanz et al. 1985). It was closed most of the time from 1972 through 1982, and the stock has never recovered to its pre-exploited condition. The rise and fall of the San Matías Gulf scallop fishery paralleled similar events in other parts of the world, e.g. the Cockburn Sound (Western Australia) *Pecten modestus* fishery in 1970–74 (Hancock 1979) and the Bahia de los Angeles (Gulf of California) *Pecten vogdesi* fishery in the mid 1970's (unpubl. data).

In the San José Gulf, small, irregular harvesting of stranded scallops has operated since the early 1950's. In the late sixties a dredging fishery developed, but the collapse in nearby San Matías Gulf prompted local regulations restricting dredging. In the mid-seventies a fishery employing commercial divers was implemented and a small diving fishery has existed since then, undergoing ups and downs resulting from general political and economical instability.

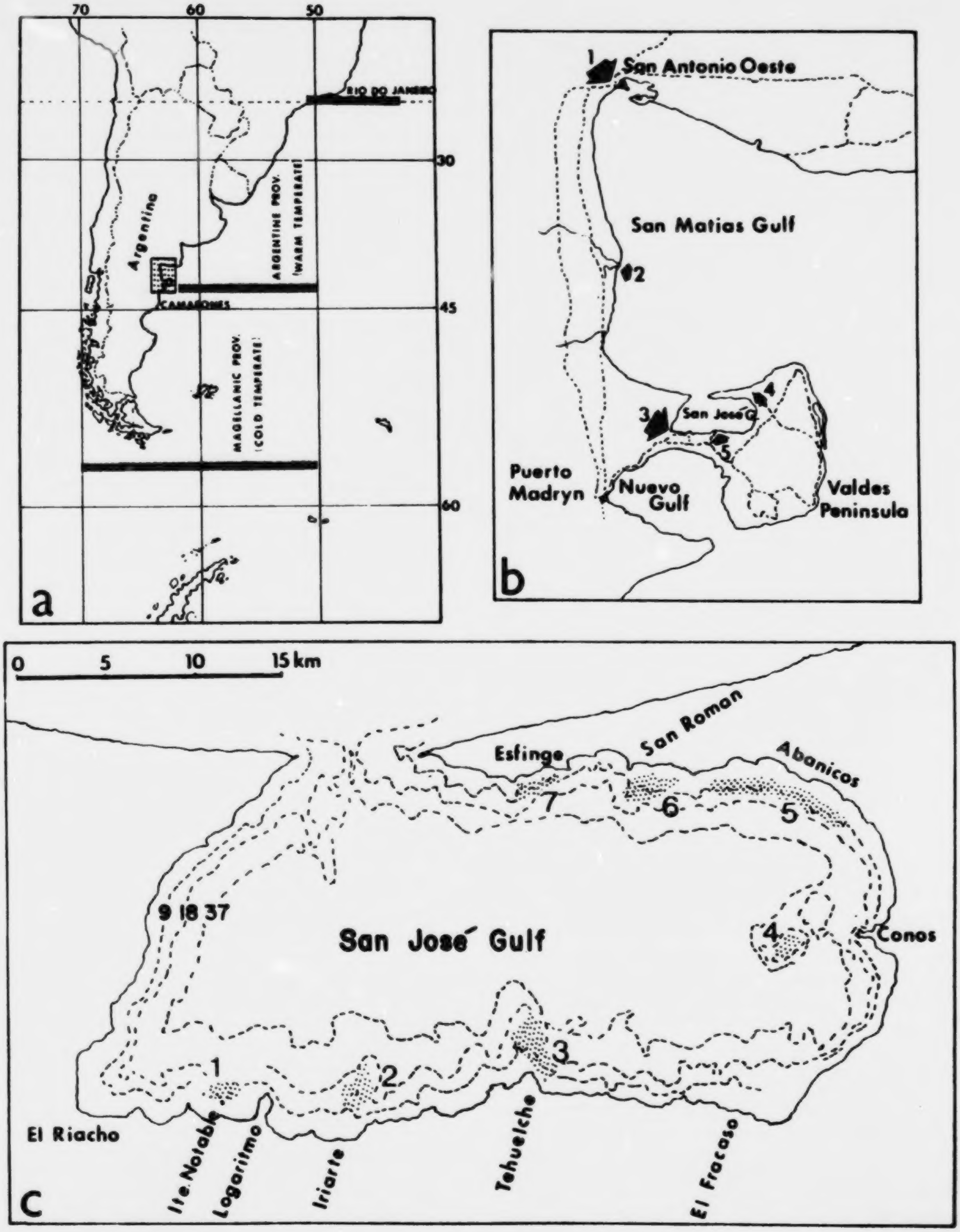
70
60
50
30
45
60
RIO DO JANEIRO
Argentina
ARGENTINE PROV. (WARM TEMPERATE)
CAMARONES
MAGELLANIC PROV. (COLD TEMPERATE)
a
1
San Antonio Oeste
San Matias Gulf
2
3
4
5
San José G.
Puerto Madryn
Nuevo Gulf
Valdes Peninsula
b
0
5
10
15 km
Esfinge
San Roman
Abanicos
7
6
5
9 18 37
San José Gulf
4
Conos
1
2
3
El Riacho
Ite. Notable
Logaritmo
Iriarte
Tehuelche
El Fracaso
c

FIG. 1. The study area. (a) The Southwest Atlantic and adjacent areas; (b) The North-Patagonic Gulfs; arrows: main scallop landing points, dashed lines: main roads; (c) The San José Gulf; shaded areas: grounds (depths in metres).

Material and Methods

1. Surveys of San José Gulf

Six surveys were conducted in San José Gulf from 1970 to 1977. Most information summarized below is from the Exploratory Surveys SANJO I–III (Olivier et al. 1974; Orensanz et al. 1985).

Diving, dredging, and trawling were employed to localize scallop concentrations. Trawling and dredging were used to obtain information from depths beyond the range of diving (mostly the slope and central basin areas). In shallow areas (< 20 m depth), two procedures were followed:

— The boat sailed in a quasi-systematic pattern. At each station, all scallops in ten 1-m^2 quadrats (sampling units) within an area of approximately 100 m^2 were taken.

— The boat towed a diver who surfaced every 5–10 min and recorded an account of his observations (nature of the bottom, physiognomy of benthic assemblages, and subjective estimate of scallop abundance).

Observations were made on the distribution of benthic biota. Non-quantitative samples were fixed in 5% buffered formaldehyde solution and preserved in 70% ethanol, sorted, and distributed for sytematic study. Recorded at each station were a list of all identifiable macro-organisms, a subjective abundance rank, and a description of the physiognomy and type of substrate. Special note was made of accumulation of dead scallop shells on the substrate, presence and abundance of scallop predators, and dominant algal genus (usually *Ulva* or *Codium*).

2. Periodic Sampling of the San Román Ground

The San Román ground was selected as the main study site, both because preliminary information indicated it had had high scallop densities in past years, and for logistic convenience (Olivier et al. 1974). Exploration of the ground with divers in November 1974 showed that density was maximal in a slightly eccentric area (ground's core), and declined irregularly towards the periphery.

A strip approximately 90 × 10 m, perpendicular to the coast, was marked in the high density area. Average depth was 8 m below the 0-isopleth. Monthly sampling trips were made regularly between November 1974 and November 1977. No samples were taken in December 1975, April, June, July, and December 1976, and April 1977. Thus 31 sampling trips were made over the 37-mo study period (Orensanz et al. 1985). On each trip the following data and samples were collected:

a) A quantitative scallop sample consisting of nine randomly picked 1-m^2 quadrats (sampling units). All scallops within a quadrat were carefully picked by a specially trained diver. This procedure removed all scallops above 25 mm shell height, but smaller sizes were incompletely sampled.

b) From November 1974 to October 1976, a random sample of scallops was taken by a diver swimming along a transect and collecting all scallops seen along his path (size bias was as above).

c) Non-quantitative sample of juveniles (0+ age class). In 1976 and 1977 settlement was poor. To search for juveniles, samples of epibenthic materials (shells, algae, invertebrates) were taken by divers and sorted for scallops in the field.

d) Simultaneously with scallop abundance, the following samples or data were obtained: scallop stomach contents and benthic microflora samples (Vernet 1977), gonads from a random subsample for histological study of the reproductive cycle (Lasta and Calvo 1978), lipid content and composition (Pollero et al. 1979), along with temperature, incident light, dissolved oxygen, concentration of nitrates, nitrites and phosphates, phytoplankton, photosynthetic pigments, and particulate carbon and nitrogen, all at three different depths (0, 5, and 10 m) (similar observations were done near Ite. Notable, Fig. 1c) (Charpy et al. 1980a,b,c).

Scallop samples were fixed with buffered 10% formalin solution in sea water, taken to the laboratory in Puerto Madryn, and processed within a week. Height (maximum diameter from the umbo to the ventral border of the shell) was measured for all specimens. All scallops from the quantitative sample (quadrats) were weighed (total weight) and aged. The reader is referred to Orensanz et al. (1985) for a complete description of aging methods and results. All aged shells are stored at the Centro Nacional Patagónico (Puerto Madryn, Argentina). In total, 21 200 specimens were measured (height) over the study period. Of these, 15 830 were aged and complete measurements were obtained from 4 500 specimens.

A complete set of measurements was taken from a subsample obtained from either the simple random sample (November 1974 through August 1976) or from the quantitative (quadrats) sample (September, October, and November 1976). The size of this subsample was around 200 (166 to 438) adult specimens. All were dissected and the following components weighed separately after draining for 5 min: shells (previously brushed and washed to remove epibionts), whole meat, adductor muscle, and gonad. Composition of epibiosis was recorded for both shells, and a subjective estimate of percent cover was made. All weights were measured on a METTLER balance to 0.1 g. All linear measurements were taken with calipers to 0.1 mm.

Wet and dry weights of different scallop fractions are highly correlated and display the same patterns of seasonal fluctuation (Ansell 1974; Taylor and Venn 1979; Lasta and Calvo 1978). Relative wet weight of the gonad, a simple gonadosomatic index, reflects the gonadal cycle; declines in index or in gonadal weight are strongly correlated with spawning (Lasta and Calvo 1978).

3. Experimental Fishing

Commercial Diving. — In February–March, 1973, a complete log was made of the activity of a crew of commercial divers fishing in the San Román ground during 12 working days. Recorded were: daily catch, number of divers fishing per-day, and, over two of the days, the size frequency distribution of scallops in the population and in the catch, and scallop density in harvested patches.

Performance of an experienced commercial diver was assessed in May 1976. Catch per unit effort (CPUE) and size frequency distribution (SFD) of the catch were measured on different grounds (different scallop densities and bottom types). CPUE was taken as catch of clean scallops obtained by the diver during 10 min of work with standard commercial diving gear. Density and SFD of the population were also estimated independently by research divers.

In May–June, 1977, the performance of a commerial diving crew (5–7 divers) fishing the Iriarte Ground (Fig. 1c) was monitored for 50 consecutive days. Number of divers and catch per diver were recorded every working day. On June 24, 1977, intensive sampling was done of the SFD of scallops in the catch, SFD of the population, and scallop density in the fished patches before and after fishing.

Dredging — Behavior and performance of the local commercial dredge were observed on May 9 (San Román Ground, Fig. 1c) and May 11 (Tehuelche ground), 1976, for a total of 14 hauls. Scallop SFDs were obtained for both the dredged population (samples taken by divers) and the catch. Behavior of the dredge and its visible impact on the ground were observed and documented photographically.

Trawling — In July 1977, fourteen experimental hauls of 1 to 1.5 hours duration were made with an otter trawl in areas too deep for commercial diving. SFDs of the catch were obtained.

4. SEPARATION OF COHORTS

In the age interval [0, 1.5 yr] a year-class can be discriminated from a SFD, since there is virtually no size overlap with older cohorts (Orensanz et al. 1985). Beyond 1.5 yr of age, cohorts were separated by means of growth rings. Since only one cohort could be discriminated in each year's recruitment, "cohort" and "year-class" are used interchangeably. Settlement peaks in early summer, and hence age of each cohort is counted starting January 1st of its first year of life.

5. DATA PROCESSING

Data were stored on magnetic tape and both raw data and statistical summaries are available from the author upon request. Original field and lab notebooks are available at the Centro Nacional Patagónico (Puerto Madryn, Argentina).

The statistical software package SPSS was used for most of the standard statistical analyses. Nonlinear curve fitting was done with the program SPSS-NONLINEAR, using Marquardt's algorithm (Robinson 1977).

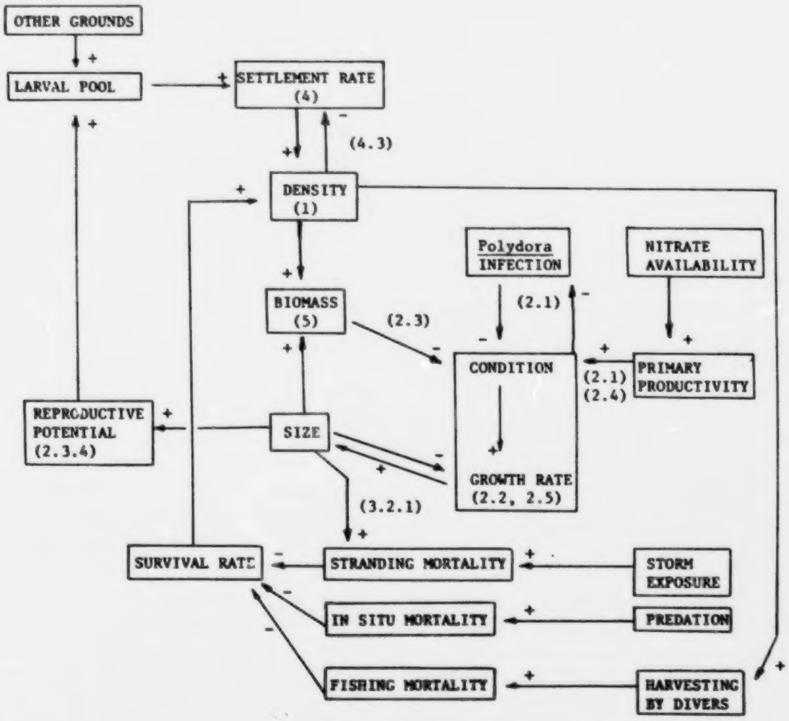
OTHER GROUNDS
+
LARVAL POOL
+
SETTLEMENT RATE (4)
+
-
(4.3)
+
DENSITY (1)
+
+
Polydora INFECTION
NITRATE AVAILABILITY
BIOMASS (5)
(2.3)
(2.1)
-
-
-
+
+
CONDITION
PRIMARY PRODUCTIVITY
(2.1)
(2.4)
+
REPRODUCTIVE POTENTIAL (2.3.4)
+
SIZE
-
+
+
GROWTH RATE (2.2, 2.5)
(3.2.1)
+
SURVIVAL RATE
-
STRANDING MORTALITY
+
STORM EXPOSURE
-
IN SITU MORTALITY
+
PREDATION
-
FISHING MORTALITY
+
HARVESTING BY DIVERS
+

FIG. 2. Schematic diagram of connections between investigated or discussed variables. Numbers within parentheses refer to Results Sections in the text.

Results

1. Distribution of the Stock

1.1 Overall Distribution

Surveys showed that the San José Gulf scallop stock is a megapopulation composed of several high-density grounds ("bancos") spread over a background of sparse density (Fig. 1c). The substock inhabiting each ground is defined as a population. Dense patches within grounds are called "beds" ("núcleos").

Different populations are interconnected by larval dispersal. This was shown by rapid recovery of grounds off the north coast of the Gulf following catastrophic depletion in 1973 (Results: 3.1).

Location of grounds has been rather constant over the years, in spite of harvesting and natural catastrophic mortalities. The San Román, Abanicos, and Tehuelche grounds have existed for at least 20 yr. The most variable are those in the SW part of the Gulf (from El Riacho to Iriarte, Fig. 1c). Populations off the North coast are exposed to stranding, which eventually reaches catastrophic proportions; few empty shells accumulate on the bottom. This contrasts with other areas (e.g. Conos) where stranding has not been reported; here the bottom is layered with dead shells.

The tehuelche scallop has catholic substrate requirements. Concentrations have been observed on sand, gravel, shell bottoms, and bare limestone terraces, but are absent from soft muddy bottoms. Substrate preference alone cannot account for the observed large-scale distribution pattern. Along the south coast there is a tendency for populations to establish at the east-northeast part of prominent points. Shelter from west-southwest winds provided by these points may enhance settlement, perhaps because of larvae being trapped in eddies.

1.2 Spatial Distribution Pattern

Mean and variance of density were calculated for each cluster of 10 sampling units and for each periodic sample (usually nine sampling units) taken at the San Román study site. Regression of log (variance) on log (mean) (Elliot 1977; Downing 1979) yielded the following values (Fig. 3a):

	Coefficient	SD
Intercept	0.2733	0.0510
Slope (b)	1.2527	0.1379

$N = 80$

$p = 1 - b/2 = 0.3736$

The exponent p was used to transform individual values. Transformation stabilizes variance and allows computation of confidence intervals for density estimates based on small samples. The spatial pattern is quite variable (Fig. 3a,b) with respect to what I have observed in other benthic bivalves (unpubl. data).

In the following sections I suggest that density plays an important role within dense patches, but larval dispersal makes local settlement at least partially dependent on conditions prevalent over the whole stock. It is then important to have at least some idea of how neighborhood (surrounding scallop) densities vary throughout the megapopulation. Figure 3c shows a density frequency distribution ($N = 373$, 1 m^2 quadrats) obtained during three surveys. Samples were taken randomly over the known distribution area of the stock (grounds and background), allowing use of the set as a simple random sample of the whole area.

For most biological considerations, density class intervals which increase in width with density are more meaningful than fixed-width intervals: it may not make a big difference to have 30 or 31 scallops per square metre, whereas a jump from 1 to 2 per square metre is very relevant. So, logarithmic density class intervals were taken, and frequencies were accordingly regrouped (Fig. 3d). Figure 3e shows the number of scallops present in each logarithmic interval, reflecting neighborhood density distribution for the whole stock. To summarize, even though the area of dense patches is comparatively small, most animals experience high surrounding densities.

2. Growth, Condition, and Reproductive Potential

2.1 Linkage Between Growth and Productive Cycle

Two aspects of the annual environmental cycle may be linked to seasonal growth: food availability and temperature. Growth during the first 1.5 yr of life (Fig. 5b) was quasi-linear and had an apparent seasonal component. So, it was further analyzed to examine growth-rate seasonality.

A linear growth curve was fitted to the height-at-date data of the 1975 cohort for the period March 1975 through March 1976 (ages 0.2 to 1.23 yr). Growth rate of young scallops seemed to reflect changes in food availability rather than temperature. Inspection of residuals (Fig. 4e, a measure of cumulative change) showed they dropped regularly from a maximum in June to a minimum in September, and then rose to a second maximum in February. This was tied to the algal productive cycle: the descending branch corresponded to winter, when phytoplankton production was low, and the ascending branch to the spring–early summer bloom (Fig. 4c,d). Residuals increased from March to June (when temperature was dropping), reflecting the small fall phytoplankton bloom (Fig. 4c, left). Finite growth rate (Fig. 4f, a measure of change over Δt) showed a consistent winter drop in June–September. A sudden rise of growth rate in September (Fig. 4f), when water temperature was at its minimum, reflected onset of the spring bloom.

The picture was more complicated for growth in weight, as this was strongly influenced by the reproductive cycle (Fig. 15a). Older specimens showed negative growth rates following spawning and, though less important, during the winter. Spawning period growth minima are reflected in the main growth rings, S_i (Fig. 15a; see Orensanz et al. 1985 for details).

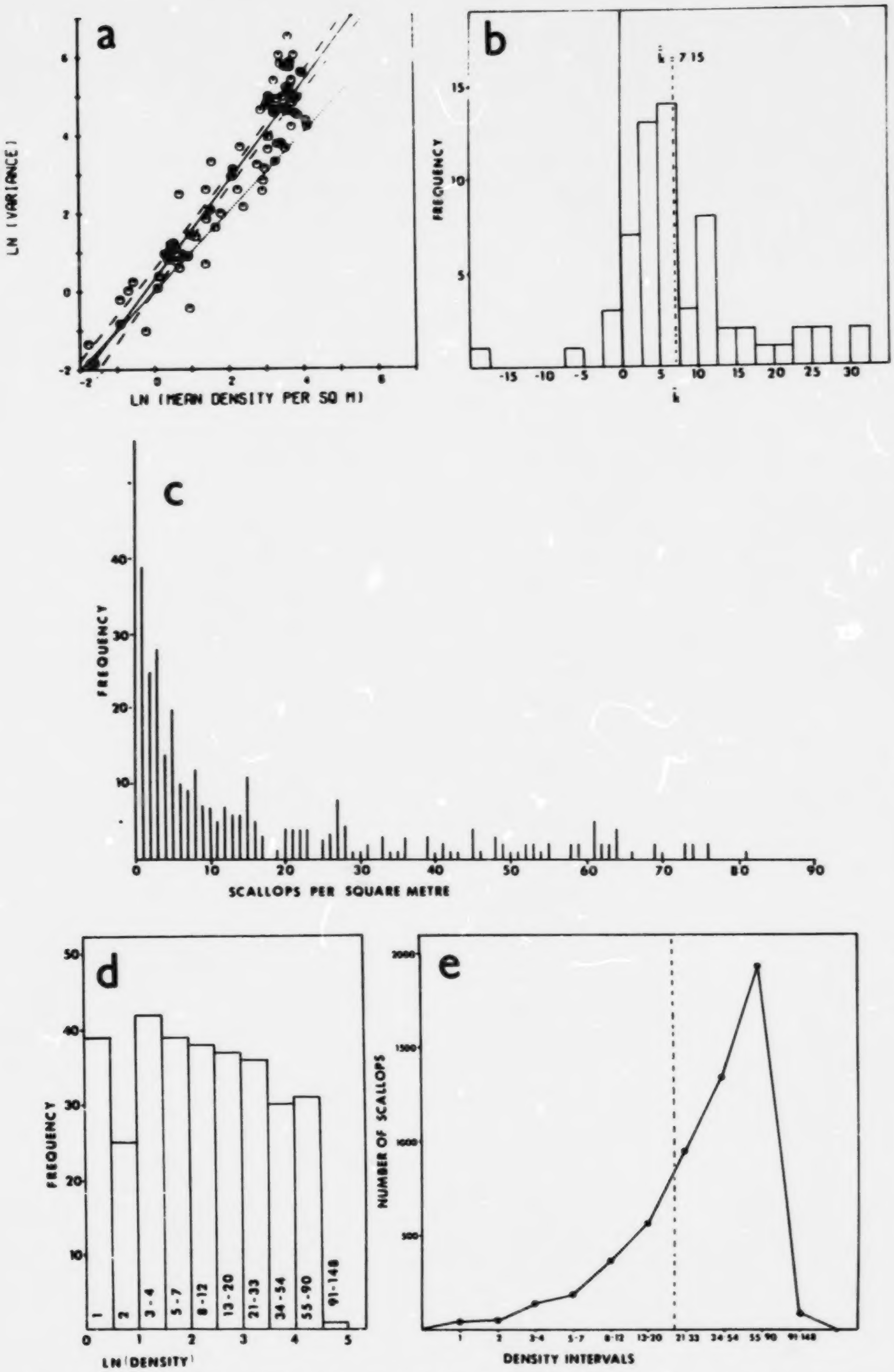

FIG. 3. Spatial distribution. (a) log (variance) vs. log (average density) for 80 samples; fitted regression line (solid line) and 95% CI (dashed line) (b) Distribution of estimated values of the negative binomial distribution "*k*" parameter; (c) Density (scallops·m^{-2}) frequency distribution based on a random sample of the whole megapopulation ($N=373$); (d) Same as (c), with logarithmic density intervals; (e) Number of scallops sampled at each logarithmic density interval; dashed line: approximate density threshold below which commercial divers stop fishing.

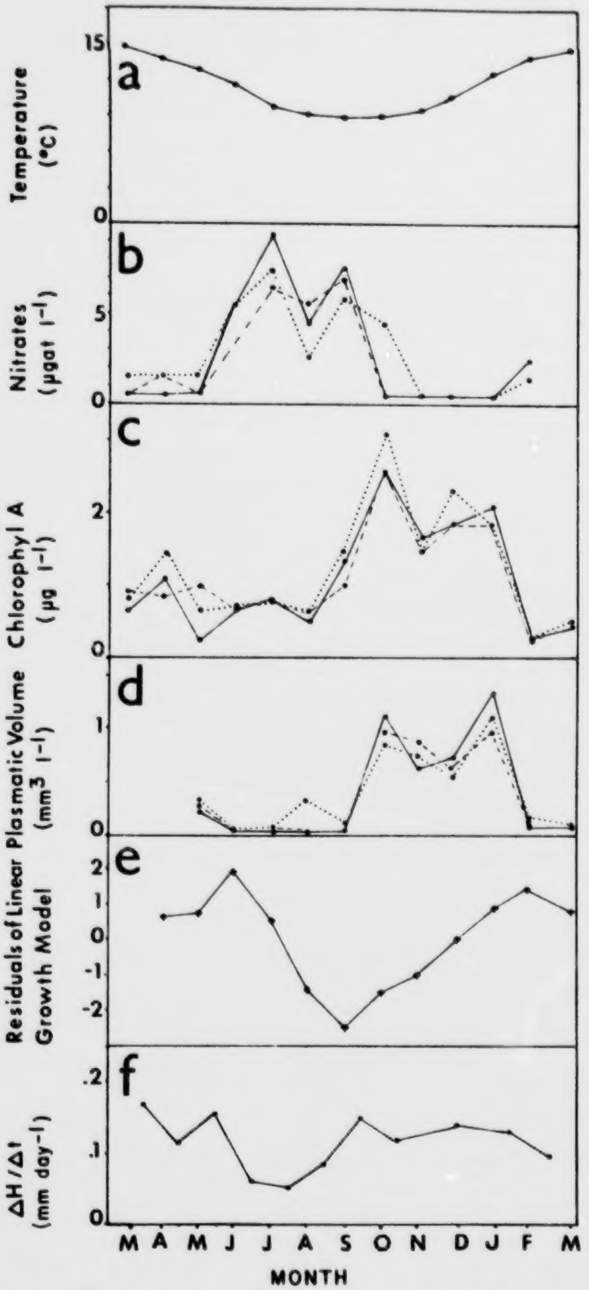

FIG. 4. Growth and oceanographic variables values at San Román, March 1975–March 1976. (a) Temperature (°C); (b) Nitrate concentration; (c) Chlorophyl *a* concentration; (d) cytoplasm volume of phytoplankton cells; (e) Residuals of a linear growth model fitted to the 1975 cohort average height (age 0+ to 1+ yr); (f) finite growth rates of the 1975 cohort (mm of height·d^{-1}); in b, c and d: (-): surface, (--): 5 m, (..): 10 m depth.

2.2 Between-Cohorts Differences in Growth in the San Román Ground Population

Two models were considered to represent growth over the whole life-span of individual cohorts (Fletcher 1973): the determinate form

(1) $y' + ay + b = 0$

and the indeterminate form

(2) $y' + ay^n + by = 0$

where, in our case, y corresponds to total height ($H(t)$). The respective closed-form solutions are

(3) $H(t) = H_\infty(1 - \exp(-k(t - t_0)))$

(4) $H(t) = H_\infty(1 - \exp(-Km(t - t_0)))^{1/m}$

where $H(t)$ is height (in mm) at time t (in years), and H_∞, k, K, n, and m are constants (H_∞ is a theoretical asymptotic height and k is known as the "catabolic coefficient"). Both are widely used in fisheries research and are respectively known as the von Bertalanffy (LvB) and Chapman–Richards (CH–R) models.

Average height-at-age data for each year-class were used in parameter estimation. Models were fitted by means of weighted non-linear regression. Weights were made inversely proportional to $\mathrm{var}(\bar{H}_i)$. Three cohorts (1973, 1974, and 1975) were represented in the samples in large enough numbers and over a long enough fraction of their life history to permit estimation of cohort-specific growth parameters.

The 1975 year-class was the strongest and was sampled monthly from shortly after its settlement to age 3. Evidence of an inflection point in the growth curve early in the life history of the cohort (Fig. 5) suggests a priori that model (2) best describes growth.

Estimated t_0 values for the CH–R and LvB models were, respectively, -0.097 and 0.12. Size of a pediveliger at settlement is about 0.3 mm. The t_s (t at settlement) etimated from each model was -6 and $+45$ d, respectively. Observed t_s was centered around the beginning of the year (Results 4.1). Thus, the CH–R model best describes the early growth pattern. The value $|\hat{t}_0 = -0.097|$ estimated for the CH–R model was not significantly different from 0. Consequently, only parameters of the version forced through $|t_0 = 0|$ are used below. Estimated t_s was 14 d, which is still reasonable.

Cohort-specific models were fitted to examine between-cohorts, within-bed differences in growth pattern, yielding the parameter values shown in Table 1. Models were compared for the three cohorts with the multivariate Hotelling's T-test (Srivastava and Carter 1982). All pair-wise comparisons between cohort-specific growth models showed statistically significant differences (see Orensanz et al. 1985 for complete numerical results).

The three cohorts grew under different and varying adult density conditions. The 1973 cohort settled during a high adult density year (Olivier et al. 1974). Later the adult population was decimated by storms (Results 3.1). Density was low when the 1973 cohort reached its second winter (1974) and, the 1974 cohort settled. When the 1975 cohort settled, average biomass was increasing and continued to rise during 1975–76 (Figs. 12c, 14).

TABLE 1. Estimated parameters for growth models fitted to the data from the San Román population. LvB = Von Bertalanffy; CH–R = Chapman–Richards.

Model	Cohort	H_∞ (mm)	k yr^{-1}	K yr^{-1}	m	t_o (yr)	ω
LvB	All pooled	82.86	0.75	—	—	0.19	
"	1973	82.32	1.13	—	—	0.78	93.3
"	1974	75.50	1.52	—	—	0.54	114.8
"	1975	77.14	0.80	—	—	0.12	61.9
LvB,$t_0=0$	All pooled	90.70	0.55	—	—	—	
"	1973	89.56	0.60	—	—	—	53.7
"	1974	84.27	0.72	—	—	—	60.9
"	1975	88.40	0.55	—	—	—	48.6
CH–R,$t_0=0$	All pooled	79.53	—	1.56	0.62	—	—
"	1973	81.82	—	5.41	0.25	—	—
"	1974	75.01	—	7.07	0.26	—	—
"	1975	70.45	—	2.30	0.55	—	—

Because of observed overall growth patterns (Fig. 5b), I examined the first year and the rest of the life history separately. Ranking of average population biomass during the first year of life of the three cohorts was 1975 > 1973 > 1974. Growth during the first year would be expected to be reflected in the value of the parameter $\omega = H_\infty k$, in the LvB model (Gallucci and Quinn 1979). Estimated cohort-specific ω and k values ranked in an order precisely inverse to biomass: 1974 > 1973 > 1975.

Beyond the first 1.5 yr of life, all cohorts grew under conditions of increasing total biomass, the ranking being 1975 > 1974 > 1973 for their second and third years of life. Thus, although the 1974 cohort experienced the lowest biomass conditions during its first year of life, it was at an intermediate position when older ages were compared. Estimated asymptotic heights of the Chapman–Richards model ranked in the opposite direction: 1973 > 1974 > 1975 (Orensanz et al. 1985).

The pattern of between-cohort differences in growth suggests density dependence as a viable hypothesis. This is further explored below.

2.3 Density Dependence of Growth and Reproductive Output

2.3.1 Within-cohort, between-patch evidence — On November 3, 1976, a sample was taken to examine size attained by individuals of the 1975 cohort in different sites of the San Roman ground. Ninety seven randomly picked, scallop-containing, 1-m^2 quadrats were taken from all over the ground. Average height was 58.9 mm. Individual measurements were pooled by scallop density strata for analyses (density range: 1–102 scallops/m^2; range of number of individuals in each stratum: 7–94; range of the $\mathrm{SD}(\bar{H})$: 2.93–7.06).

If there were a density-dependent component to growth, it might be reflected in different growth rates of individuals in patches of different density. Average height of the 1975-cohort was negatively correlated with adult (1+ and older) density ($r^2 = .58$, $P < .01$, $N = 36$). Density thus seems to explain a considerable fraction of local variations in growth (25% for individual scallops, $P \sim 0.00001$, $N = 1392$; Orensanz et al. 1985). Other factors potentially contributing to observed variation are site-quality gradients or local differences in timing of settlement, neither of which were measured.

2.3.2. Between-cohorts, within-site evidence — The 1974 and 1975 cohorts were sampled throughout their whole second year of life at the same study site. At the end of their first year, both were about the same height, (Fig. 6e,h), but during their respective second years the

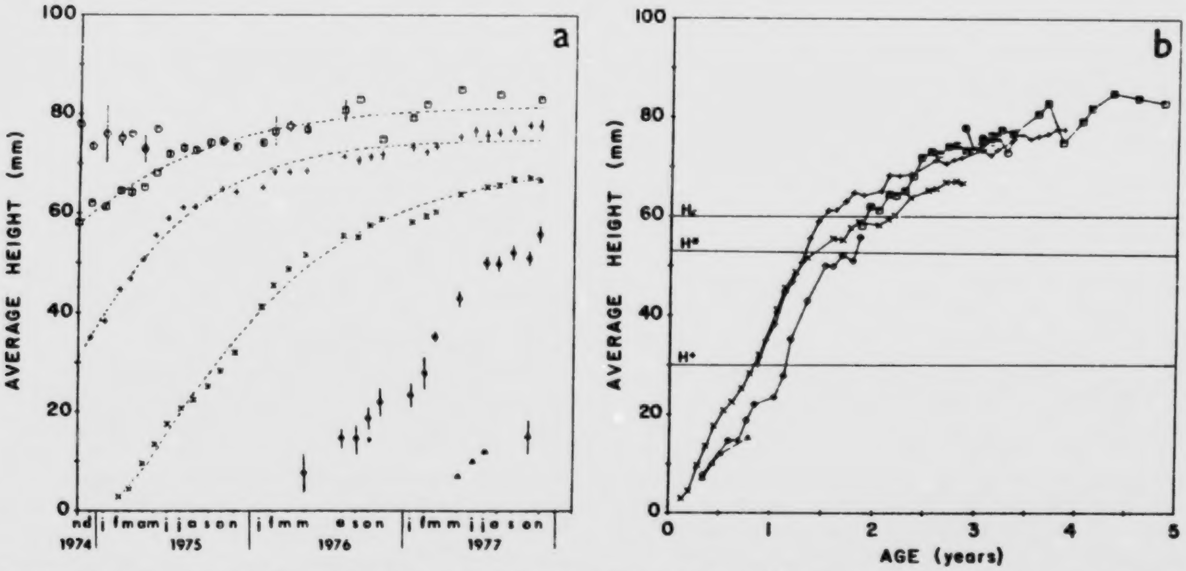

FIG. 5. Cohort-specific growth patterns. (a) Average cohort size over the 3-yr study period; dashed lines: Chapman–Richards functions (with $t_o = 0$) fitted to the 1973–75 cohorts; (b) same at age; horizontal lines: average sizes at which the cohort is recruited to the quantitative sampling technique ($\bar{H}+$), to size-dependent mortality $\bar{H}^*$), and to commercial size ($\bar{H}c$). Symbols for each cohort are (○) 1972, (□) 1973, (+) 1974, (×) 1975, (◇) 1976, (△) 1977.

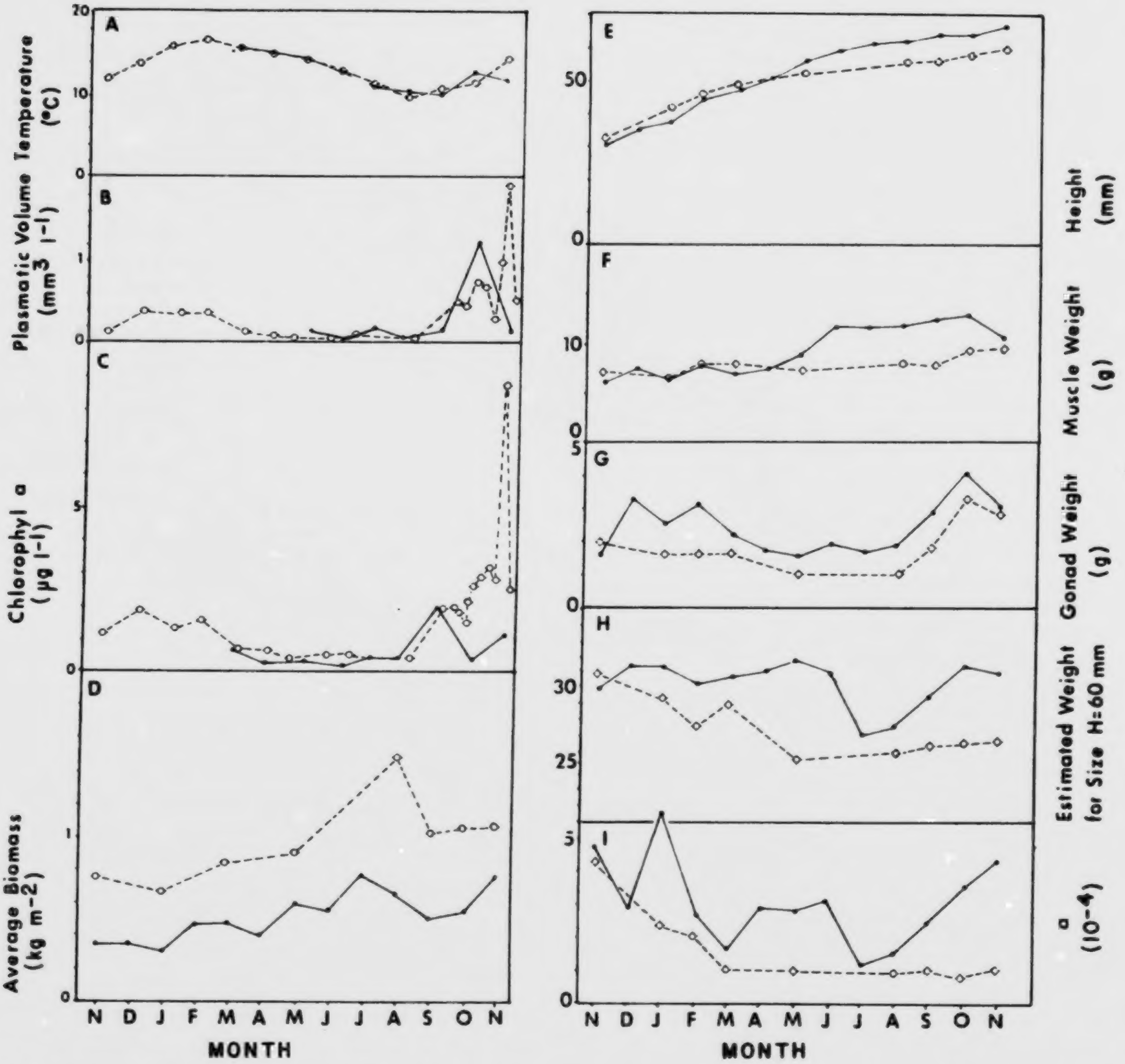

FIG. 6. Contrasts between the 1974 and 1975 cohorts, and between environmental conditions experienced during their second year of life. Dates are Nov.1974–Nov.1975 for the 1974 cohort (solid lines), Nov.1975–Nov.1976 for the 1975 cohort (dashed lines). (A) temperature (°C); (B) phytoplankton cytoplasm volume; (C) chlorophyll *a*; (D) average total (all cohorts, total weights) biomass; (E) average height; (F) average muscle weight; (G) average gonad weight (g); (H) weight (g) of a 60-mm height specimen estimated from the monthly fitted allometric height:weight relationship; (I) Intercepts of the monthly fitted [height vs. weight] allometric relationship. B and C are averages for the three sampled depths (0, 5, and 10 m) at Ite. Notable.

1974 cohort grew faster than the 1975 cohort. This shift was first reflected by weight of the gonad (Fig. 6g), and later by weight of the muscle (Fig. 6f) and height of the shell (Fig. 6e). The difference was also reflected in coefficients of a power function fitted to the height: weight relationship (Fig. 6h,i).

Two alternative hypotheses on causative factors would reasonably explain the observed divergence: (a) differences in environmental conditions and/or food supply, and (b) differences in population density.

Several environmental variables were measured at a neighboring station (Ite. Notable) during the entire Nov. 1975–Nov. 1976 period, and most of the Nov. 1974–Nov. 1975 period. The same variables were determined between March 1975 and March 1976 over the San Roman ground (Fig. 4): seasonal variation in both stations showed the same pattern (compare Fig. 4 and 6). I could find no evidence to support hypothesis (a): water temperature, phytoplankton cytoplasm volume, and chlorophyll A concentration (Fig. 6a,c) were similar for both years, or were even "better" during 1976 than during 1975.

Average biomass was consistently higher in 1976 than in 1975 (Fig. 6d). This is compatible with hypothesis (b). Growth rate seemed to be detectably depressed above 1 $kg \cdot m^{-2}$ average biomass.

2.3.3. Density-dependent growth rate — Finite per-day average size increments for each represented cohort ($\Delta\bar{H}/\Delta t$; where $\bar{H}$ is average height in mm, and t is time in days) were estimated for all pairs of consecutive sampling dates that were at most one month apart from each other, and for which the number of scallops was greater than 10 in both samples.

The ($\Delta\bar{H}/\Delta t$) values were well scattered around the growth rate vs. size curve generated with parameters of the Chapman–Richards model (pooled cohorts). Deviates (whether standardized or not) from that average model were negatively correlated ($r = -0.22$, $0.01 < P < 0.05$, $N = 59$) with the corresponding total average biomass values,

$$\bar{B}(t_i,t_{i+1}) = (\bar{B}(t_i) + \bar{B}(t_{i+1}))/2, \quad i = \text{sampling date}$$

This was also the case if a non-linear curve fitted with finite rate values was used.

The difference equation

$$(5) \quad \Delta\bar{H}/\Delta t = a\bar{H} + b\bar{H}^n + c\bar{H}\bar{B},$$

where $\bar{H}$ is average height in mm, t is time in years, $\bar{B}$ is average biomass over Δt in $g{\cdot}m^{-2}$, and a,b,c and n are constants, was fitted to size-increment data of all cohorts. Estimated parameter values were:

$$[a = 14.52,\ b = -4.64,\ c = -0.00016,\ n = 0.75]$$

Equation (5) was used to introduce density-dependent growth in simulation trials.

2.3.4 Density-dependent depression of reproductive output — If growth rate and weight at size (condition index) were depressed at high densities, a corresponding drop in reproductive output might be expected. Increase in gonad weight from winter to spring corresponds mostly to proliferation and growth of gametes. Thus, the difference in gonadal weight between spring maximum and the preceding winter minimum is an index of reproductive output. Values estimated for 1+ and 2+ year-classes, and for the respectively low- and high-density years 1975 and 1976, showed a relative drop in reproductive output of 80% for the 1+ and 25% for the 2+ age group (see Orensanz et al. 1985, for tables of gonadal weight).

2.4 Between-Ground Contrasts

Several environmental variables showed a well defined spatial gradient in the Gulf from the mouth (NW corner) to the SE corner (Fig. 7a,b). Temperature tended to increase in summer (Boschi and Fenucci 1972), and to decrease in winter (Pizarro 1975), and nitrate content in May 1976 decreased (Fig. 7b). Isolines (Fig. 7a) of percent "San José water", based on the TS-curve (Pizarro 1975), displayed a similar picture.

2.5 Growth in Weight of Different Body Fractions

Figure 8 shows growth in weight (partitioned by fractions) of the 1974 cohort during its first 3 yr of life. After 1.8 yr, most growth in weight was accounted for by the shell. Average shell weight grew at a rather constant rate during the first 3 yr of life for all cohorts studied. The shell weight:meat weight ratio tended to increase slightly with age (Orensanz et al. 1985), and was a simple and useful index of condition. It was easy to measure and fluctuated around 1, reflecting changes in condition associated with spawning and season. It also showed the density-related poor condition of the 1975 cohort:

Cohort	Age	Period	Average shell/meat ratio
1974	2+	Jan.–Nov. 1975	0.992
1975	2+	Jan.–Nov. 1976	1.132

Adductor muscle (the portion exported to the US) is classified by industry in 3 size classes (Orensanz et al.

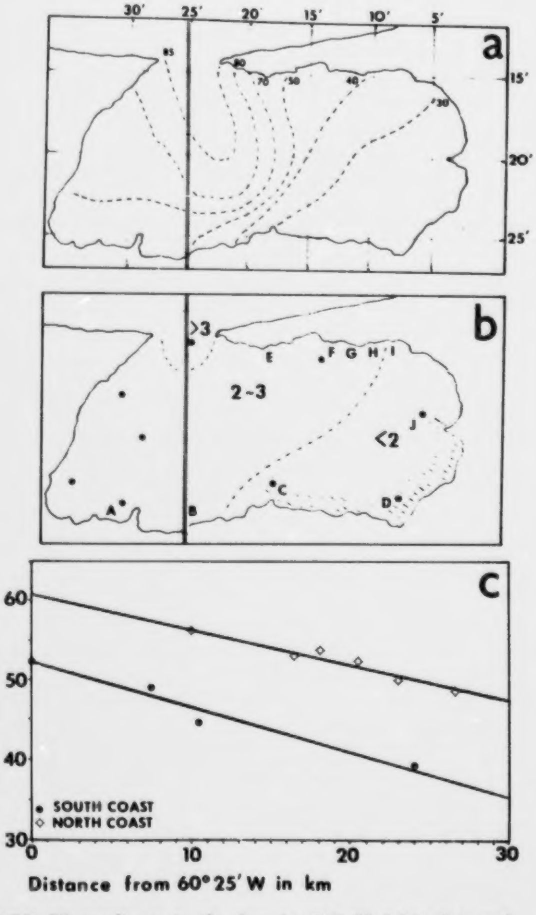

FIG. 7. NW–SE gradients in the San José Gulf. (a) isolines of percentage of "San José water"; (b) Nitrates in May 1976; * = oceanographic stations of the *Sanjo II* Survey; A–E = collection sites for scallop samples presented in (c); shading = area where *Codium* replaces *Ulva* as the dominant sublitoral seaweed; (c) average height of the 1975 scallop cohort in May 1976, plotted against the distance in km from the 60°25" meridian.

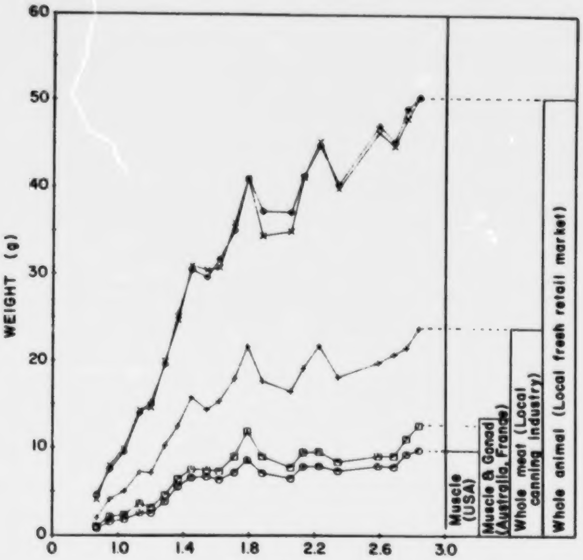

FIG. 8. Tissue weights (g) from the 1974 cohort. Right-hand scale indicates products consumed by different markets. (◇) total weight; (×) meat + shell; (+) all meat; (□) muscle + gonad; (○) muscle.

1985). For all cohorts studied, average muscle weight was about one standard deviation above the lower boundary of the smallest size class (minimum commercial size) 2 wk after the average height of 60 mm had been reached. This minimum commercial size was normally reached during the second year of life, but the timing varied greatly and seemed, as other aspects of growth, related to population density. The 1974 cohort, which grew during a period of low density, reached commercial size early (1.4 yr), while the 1975 cohort, which grew during a period of high density, reached the same size around its second birthdate. This was reflected in the relative weight of muscle yielded by the scallops: around 20% during the winter of 1975 (a low density period), but less than 15% during the winter of 1976 (a high density period). On the average, tehuelche scallop muscles fell in the medium size standard for most of their life, but the 1973 cohort (which spent its third year under low density conditions) fully entered the "large" standard at 2.4 yr (see Orensanz et al. 1985, for illustrations and tabulated numerical results).

Muscle weight also has a seasonal fluctuation, related to the primary production cycle and to spawning season. Growth curves for muscle and gonad for the Nov.74–Nov.75 period (low biomass) were similar for the two age classes represented (Orensanz et al. 1985). Muscle grew rapidly during the fall, did not grow during the winter, grew slightly in late-winter/early-spring, and lost weight in phase with the gonad following spawning.

Is this gradient paralleled by attributes measurable in scallop populations? Because their food may be affected, growth was examined. There were marked differences in size-at-age (obtained from growth ring data; Orensanz et al. 1985) among different grounds, and the emergent pattern paralleled the ones outlined above. Values of the LvB model parameters estimated for five populations for which at least four age classes were represented in samples taken during the SANJO-II Survey were:

	Ground	k	H_∞	ω
North coast	San Román	0.65	87.4	56.8
	Abanicos	0.65	84.8	55.1
	Pta. Conos	0.71	77.4	54.9
South coast	Ite. Notable	0.56	90.4	50.6
	Pta. Tehuelche	0.67	73.1	48.9

Estimated asymptotic height and ω decreased as distance from the mouth increased along each coast.

Average heights ($\bar{H}$) attained by the 1975 cohort in May 1976 in different beds (Fig. 7c) were compared. The North and South coasts were treated separately, and distances were taken from the 64°25′W meridian (Fig. 7a,b). Largest average sizes were observed near the meridian, the minimum was at the SE corner (El Fracaso), and the other samples fell between these extremes (Fig. 7c).

These patterns match hydrographic gradients mentioned above. The observation is consistent with the hypothesis of a reduction in food supply from NW to SE, as the distance from the sole external source of nutrients (the Gulf's mouth) increases.

Fluctuations in weight of the gonad followed the reproductive cycle, with winter minima and spring maxima. The timing of the spring spawning peak differed from year to year, ranging from October (1975) to December (1974). The relative weight of the gonad was low for the 0+ age group (Orensanz et al. 1985).

Part of the gross scallop weight was composed of epibionts. Among these, the most frequent were monaxonid sponges, encrusting coralline algae, *Ulva* and a few other algae, the spirorbid polychaete *Paralaeospira levinseni*, the serpulid polychaetes *Hydroides plateni* and *Apomatus* sp., and barnacles. An unidentified purplish monaxonid sponge was the first epibiont to develop. Most of the other components colonized the shells during the scallop's second summer, as they entered the 1+ age group. Spirorbid and serpulid polychaetes were preferentially found on the lower valve, and *Ulva* and other algae on the upper valve. Monaxonid sponges, encrusting coralline algae, and barnacles were spread over both valves. A comparison of the different grounds showed that the epibiont load varied from ground to ground, and was lowest at the San Roman ground (Fig. 11; Results: 3.2.3).

2.6 Growth and *Polydora* Infection

Micro-crevices which form the growth rings (Results 2.1) facilitate settlement of the shell-boring polychaete *Polydora*[1]. *Polydora* infection was directly related to poor condition. The 1975-cohort experienced a density-dependent depression in growth rate (Results 2.2), and rate of infection was the highest seen for the San Román Ground. A slightly negative shell growth rate (produced by the erosion of deteriorated shell borders) was measured during the spring of 1976.

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[1] The species is *Polydora websteri* Hartman, which has been reported from both coasts of North America (Blake and Evans 1973) as a pest of several commercially important bivalves, including calico and giant scallops (*Aequipecten gibbus* and *Placopecten magellanicus*). This is the first record of this spionid polychaete for the southwest Atlantic Ocean.

3. MORTALITY

3.1 Sources

Beach Stranding — This was the main source of mortality along the north and northeast coasts of the Gulf, operating in a pulse-like fashion. Stranded animals were the subject of a small, irregular commercial fishery, and many were eaten by sea-birds or simply died from desiccation. Large strandings occurred when winds from the SE quadrant blew during at least one complete tidal cycle. Such events are generally rare. Their average frequency fluctuates seasonally, with maxima in January, March and November (Orensanz et al. 1985). Hundreds of tons of scallops were stranded in 1973. Olivier et al. (1974) reported high densities of scallops for the San Roman ground in February, 1973. Following the great 1973 strandings, a search (J. Picayo, pers. com.) failed to locate any concentration of adult scallops in the same area. An exploratory survey in August 1974, found only moderate densities of 0+ and 1+ age scallops (1973 and 1974 year-classes), but virtually no older individuals: no remnants were left of the huge 1970 year-class, which dominated the population until the summer of 1973.

Juvenile scallops are always found attached to some substrate by byssal filaments. As the animal grows attachment becomes less permanent and proportionally weaker, as has been found in other species (Caddy 1972). On November 2, 1976, a sample of the 1975 cohort was split into "attached" and "unattached" groups. Size of the unattached animals was larger than that of the attached ones,

	$\bar{X}$	Var.	N
attached	58.63	7.728	68
unattached	60.17	8.029	17

Ho: $\bar{X}a = \bar{X}u$, *Ha*: $\bar{X}a < \bar{X}u$

$t = 2.69$, df $= 69$, $P < 0.01$, Ho rejected

suggesting the existence of a within-cohort size-dependent gradient of attachment. Attached animals might be less exposed to bottom currents than unattached ones. If so, then stranding mortality would be size-dependent, with increased mortality at larger sizes associated with loss or loosening of byssal attachment.

Predation — A seastar (*Cosmasterias lurida*), a volutid snail (*Odontocymbiola magellanica*), and an octopus (*Enteroctopus megalocyathus*) were seen preying upon scallops during the course of this study but, at least in the San Román ground, their densities were low and never constituted an important mortality source.

Overcrowding — Bottom water movements tended sometimes to concentrate scallops in depressions on the bottom. In the spring of 1977 on the Iriarte ground, large numbers of scallops were trapped and piled in several layers deep into long, natural ditches, and a high proportion died, presumably of suffocation. Their decomposition created an anoxic environment over large patches of the ground. The phenomenon was never observed in the San Román ground.

Other factors — Olivier et al. (1974) found animals in poor condition or recently dead in February 1973, in the San Román ground, without identifying the mortality source. In situ mortality peaked at late winter/early spring in 1975 and 1976, following the winter combination of low temperatures, reduced primary production and poor condition of the animals.

3.2 Assessment of mortality

3.2.1 Decay of the 1973, 1974, and 1975 year-classes — When average density of each cohort was plotted against its age (Fig. 9a), a decay was not displayed until a certain age or average individual size (threshold size, $\bar{H}^*$, in what follows) was reached. When the three cohorts were contrasted, decay did not seem to proceed at the same rate.

I suggest that individual size is related to mortality rate. The implication is that average individual size rather than age should be the best overall predictor of survival. Figure 9b shows average density plotted against average individual size for the three cohorts considered. The threshold size was similar for different cohorts, and slopes of log (average density) versus average individual height were similar beyond that threshold size.

To determine objectively the average threshold size ($\bar{H}^*$) an $\hat{H}^*$ value was first guessed from inspection and was used to split the data into two subsets. Linear regression was used to fit straight lines to each subset. The value of $\bar{H}^*$ for which the total RSS of the linear models was a minimum fell within the interval 52 mm $< \bar{H}^* < 54$ mm (Fig. 9b).

Two hypotheses might explain the observed pattern; (a) incomplete recruitment to the sampling device below the threshold size $\bar{H}^*$, or (b) a change in survival rate at that size. Complete recruitment size to our sampling technique was below 30 mm, so (a) is unlikely. Hypothesis (b) is compatible with our empirical knowledge of the system. Young scallops (below $\bar{H}^*$) were presumably less exposed to current-induced mortality because most individuals were attached to the substrate by byssal filaments.

In summary, the life history of a scallop cohort can be divided in two periods, defined by average individual size boundaries:

30 mm $< \bar{H} < 52$ mm: mortality was low (it was not significantly different from 0 for the 1974 and 1975 cohorts).

$\bar{H} > 52$ mm, for which decreasing abundance was apparent, but seemingly different from cohort to cohort.

Mortality factors are poorly known and rates could not be estimated for $\bar{H} < 30$ mm.

Different cohorts reached these two sizes at different ages (Fig. 5b; Orensanz et al. 1985):

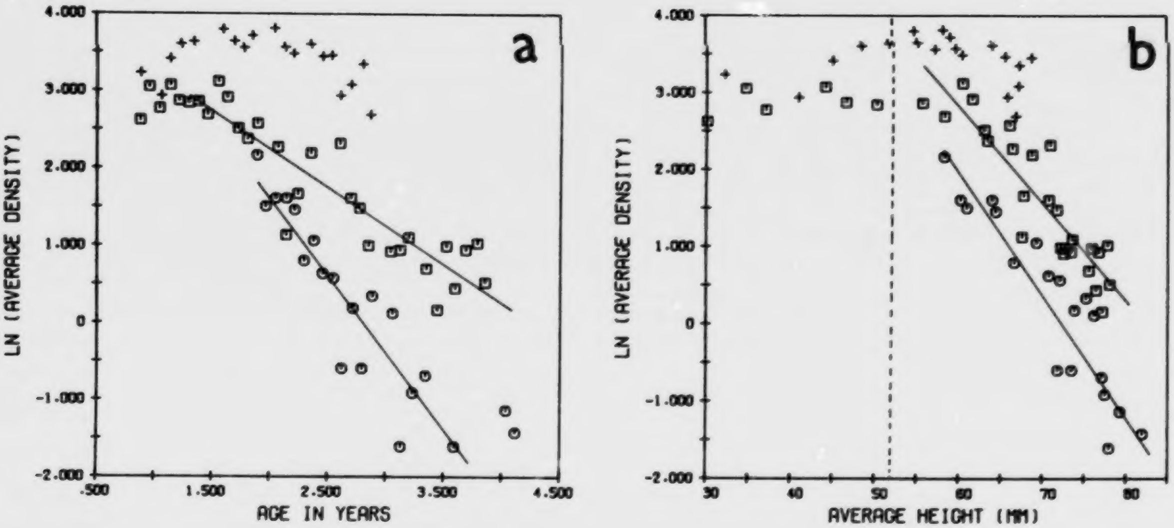

FIG. 9. Density (scallops·m^{-2}) as a function of (a) age and of (b) size. (○) 1973, (□) 1974, (+) 1975 cohorts.

Cohort	Age at $\bar{H}+$ (30 mm)	Age at $\bar{H}^*$ (52 mm)
1973	1.23 years	1.69 years
1974	.87 "	1.30 "
1975	.83 "	1.36 "
1976	1.14 "	1.79 "

Per capita instantaneous natural mortality rates (M) were estimated for each cohort from regression of log (density) on age. Results were as follows ($\hat{M}$ in yr^{-1}):

	$\hat{M}$	SE	95% CI	N (sampling dates)
1973 cohort	1.9846	0.1775	2.3518,1.6174	25
1974 cohort	0.9974	0.0953	1.1946,0.8002	25
1975 cohort	0.6198	0.1355	0.9151,0.3245	14

To test whether mortality differed between cohorts, a covariance analysis was performed with multiple regression, with log (density) as the predicted variable, age (in years) as the covariate, and year classes as factors. The hypothesis of equal slopes was rejected ($F=12.5$; d.f.:2,58; $P<0.01$). Slopes for the 1973 and 1974 cohorts (the two represented for most of their adult lifespan, Fig. 9a) differed significantly ($F=22.5$; d.f.:1,48; $P<0.01$). An equivalent covariance analysis with size instead of age as the covariate showed a non-significant difference between slopes ($F=2.3$; d.f.:2,53). Cohorts under scrutiny exhibited different growth patterns (Results: 2.2). The rank of sizes beyond |age = 1.5 yr| (Fig. 5b) was inverted with respect to that of $\hat{M}$ values. This is consistent with the hypothesis of size dependent mortality.

To represent the size-dependence of mortality succinctly, I examined the relationship between per capita finite rate of density change and average individual size. The linear relationship

$$(6)\quad \frac{\Delta \bar{N}/\Delta t}{\bar{N}} = \alpha - \beta(\bar{H})$$

where $\bar{N}$ is density (average #/m^2, by cohorts), t is time in days, $\bar{H}$ is average individual size in mm, and α and β are constants, was fitted to the data. The $\bar{N}$ values were slightly smoothed by means of a weighted ×3 moving average (weight being inversely proportional to the Δt between consecutive sampling dates). The null hypothesis $\hat{\beta}=0$, meaning that the per capita mortality rate is constant, was rejected (H_a:$\hat{\beta}<0$, $r^2=0.11$, $P=0.006$, $n=56$). The estimated values of the coefficients were

$\hat{\alpha}$ = 0.000276, SE = 0.0001062
$\hat{\beta}$ = 0.014989, SE = 0.0073884
$\bar{H}^*$ = $\hat{\beta}/\hat{\alpha}$ = 54.3 mm

The ratio ($\hat{\beta}/\hat{\alpha}$) yields another estimate of $\bar{H}^*$ (the threshold size, where mortality is expected to drop to 0) which is close to the interval |52–54 mm| estimated above. Covariance analyses with the three cohorts as factors showed no significant difference between slopes ($F=1.1$, d.f.:2,50) or factors ($F=2.58$, d.f.:2,52) when the three cohorts were compared.

3.2.2. Detection of in-situ mortality pulses — After a scallop dies, its shells ("cluckers") remain held together for a while by the ligament. Relative abundance of cluckers can be used to estimate in-situ mortality (Dickie 1955; Merrill and Posgay 1964; Marti et al. 1982), provided average time over which the valves are held together by the ligament can be estimated. Average clucker "life" (τ_c) can be obtained from the difference in the average individual size between simultaneous samples of cluckers and live animals, given an independent etimate of individual growth rate and under assumptions of constant growth and mortality rates (which are reasonable if τ_c is short).

Field observations suggested that in-situ, stress-related natural mortality increased following periods of poor condition, coincidently with growth deceleration and growth-ring marking. Such periods were centered around late winter/early spring and mid summer.

On October 5, 1976 (early spring), both cluckers and live animals belonging to the 1975 year-class were measured:

	$\bar{H}$	SD	n
Live animals	57.72	4.26	316
Cluckers	56.58	4.15	63

The estimated average clucker life (average time over which cluckers accumulated) was $\tau_c = 28$ d. Estimated $\hat{M}$ for that period was 1.2275 yr^{-1} if estimated from the drop in average density from September 7 to Octobr 5 ($\Delta t = 28$ d), and 1.2379 yr^{-1} for the clucker method ($\tau_c = 28$ d). Both values are well above the 1975 cohort average (0.62 yr^{-1}; 95% CI:.32,.91), and close to each other. In February, 1973, large numbers of fresh cluckers were observed (Olivier et al. 1974). Using the value of τ_c estimated above and the recorded clucker:alive ratio (52:279) yields $\hat{M} = 2.3$ yr^{-1}, which is relatively high.

These figures, although crude, show that clucker information can be effectively used to detect in situ mortality pulses, and that these follow periods of physiological stress.

3.2.3. Effects of mortality on size frequency distribution — If mortality were size-dependent one would see contrasts in mortality among cohorts and also between individuals of different sizes within each cohort. This would be reflected in changes in the cohort's size frequency distribution. Size selective mortality should be associated with depressed variances at larger sizes. Observed values of the standard deviation of height were consistent with that prediction (Fig. 10a,b): they decreased for age >~1.5 yr and $\bar{H}$>~50 mm.

Epibionts effectively increase the size of a scallop. If there were a size-dependent component in stranding mortality, then individuals strongly colonized by epibionts should be selectively removed from exposed beds. That this is the case was suggested by the fact that epibiont biomass per unit of shell area did not increase with age in San Román (exposed to stranding, Fig. 11a), but did in non-exposed areas like Conos (Fig. 11c). Between-grounds differences in composition of the epibiotic assemblage were not evident. Lack of accumulation of epibionts in San Román is consistent with the hypothesis of selective removal of the most fouled specimens.

4. Settlement and Recruitment

4.1 Settlement: Timing and Primary Substrate

In the San Román ground, all cohorts studied seemed to have similar settlement timing: see for example the convergence of the curves of the 1974–77 cohorts at the lower left corner of Fig. 5b. Settlement recurrently peaked around the beginning of the year (early summer), as shown by the following data:

Cohort	Date	$\bar{H}$ (mm)	SD	N	Age
1973	25/02/1973	3.17	0.92	41	56 d
1975	18/02/1975	2.95		49	49 d

This was also shown by experimental spat collection (Ruzzante and Zaixso 1984). No evidence was found of a second (late summer/early fall) settlement peak.

Most recently settled scallops were attached to the alga *Ulva* sp., which formed seasonal beds over large shallow subtidal areas. Other natural collectors (though less important) were shell hash, and rarely the shells of living adults. Juveniles detach from the algae and reattach to other bottom materials (gravel, cobbles, empty shells, polychaete tubes).

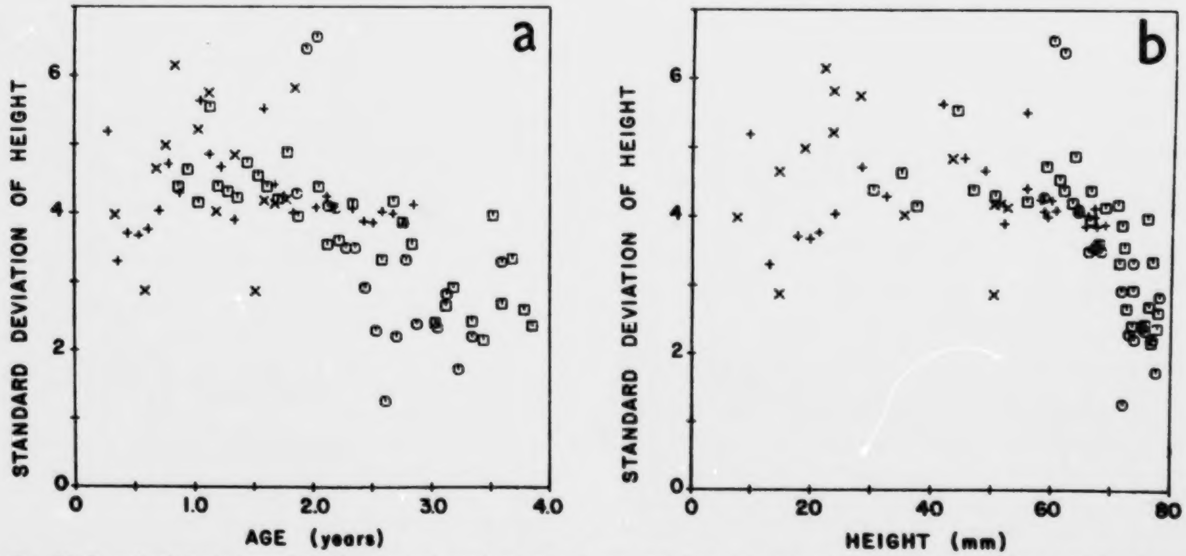

FIG. 10. Standard deviation of height (mm) plotted against (a) age and (b) average height. (○) 1973 (□) 1974 (+) 1975 cohorts.

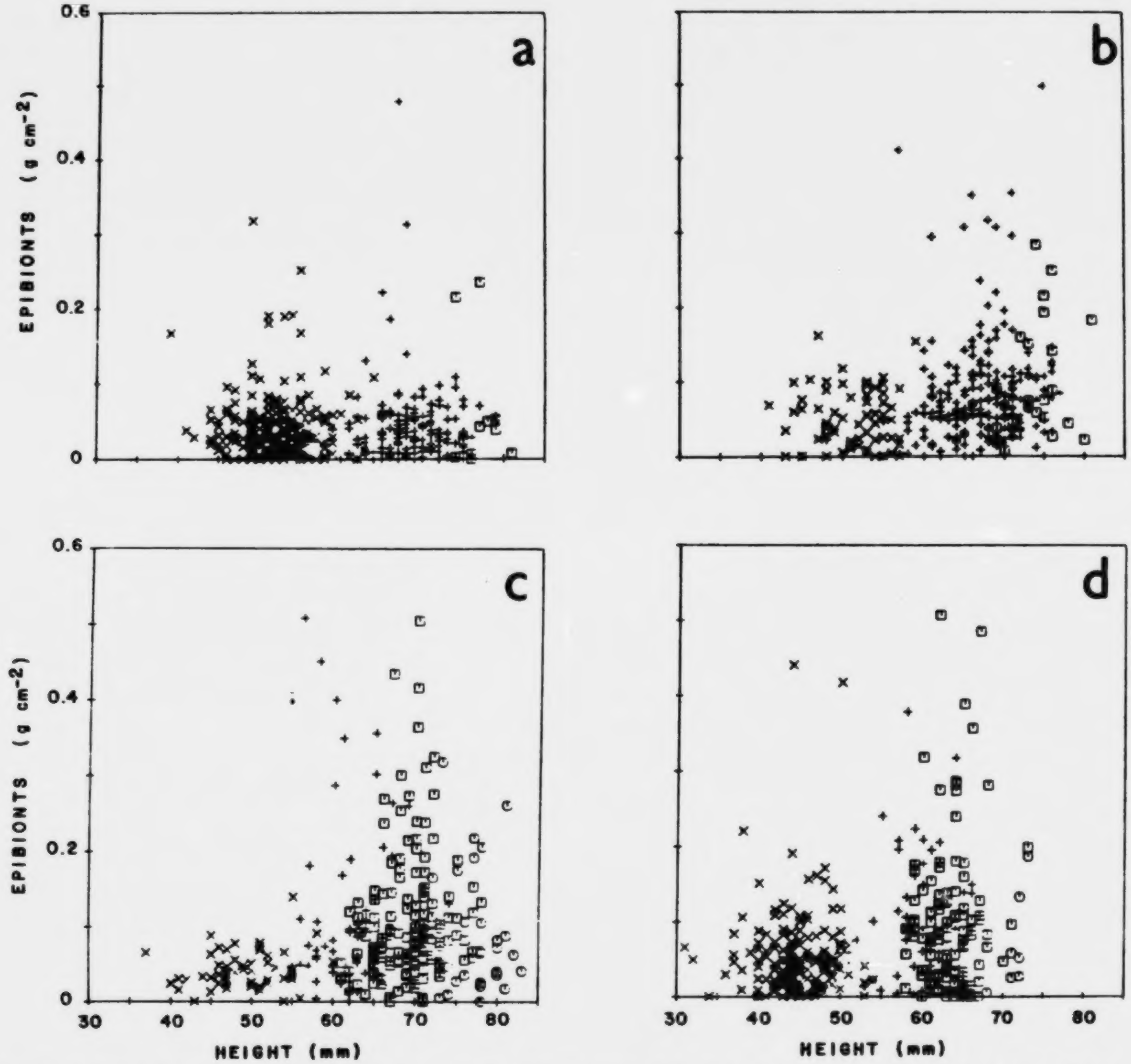

FIG. 11. Epibionts (g mm^{-2}) of projected shell surface in different grounds, May, 1976. (a) San Román; (b) Abanicos; (c) Conos; (d) Tehuelche. (×) 1975, (+) 1974, (□) 1973, (○) 1972 cohorts.

Ulva beds are frequently detached by storms and tidal currents, and drifting masses of algae often get stranded along the beaches, causing death of the attached scallop spat. Algal drift may also play a role in redistributing juvenile scallops over the bottom.

4.2 Time Series of Year-Class Strength for the San Román Ground

Historical evidence shows that in the high density core of the San Román ground a few year-classes have been extremely large, and others virtually non-existent. In February 1973, the population was dominated by the strong 1970 cohort (Olivier et al. 1974). During the study period (1974–77) another strong year-class settled in 1975. N. Ciocco (pers. com.) followed the growth of a third exceptional cohort, settled in 1980, during the years 1980–83.

I attempted to quantify relative strength of different year-classes for which information is available, covering a 15-yr period in total. Estimated average density for the size interval 30 mm $< \bar{H} <$ 52 mm (the "survival plateau" period), $\bar{D}^*$ (scallops m^{-2}), was used as an index of year class strength (Orensanz et al. 1985). The following pattern emerged (Fig. 12a):

a) Year-classes 1970, 1975 and 1980 were much larger than the rest.
b) These strong year-classes were always followed by 2 or 3 very weak year-classes (1971–72, 1976–77, and 1981–83).
c) They were preceded by year-classes of intermediate strength (1969, 1973–74, and 1978–79).
d) The three robust year-classes reached a similar $\hat{D}^*$, and were evenly spaced over time.

There was an apparent cyclicity, with constant amplitude and a wave length of 5 yr. Such a pattern can be

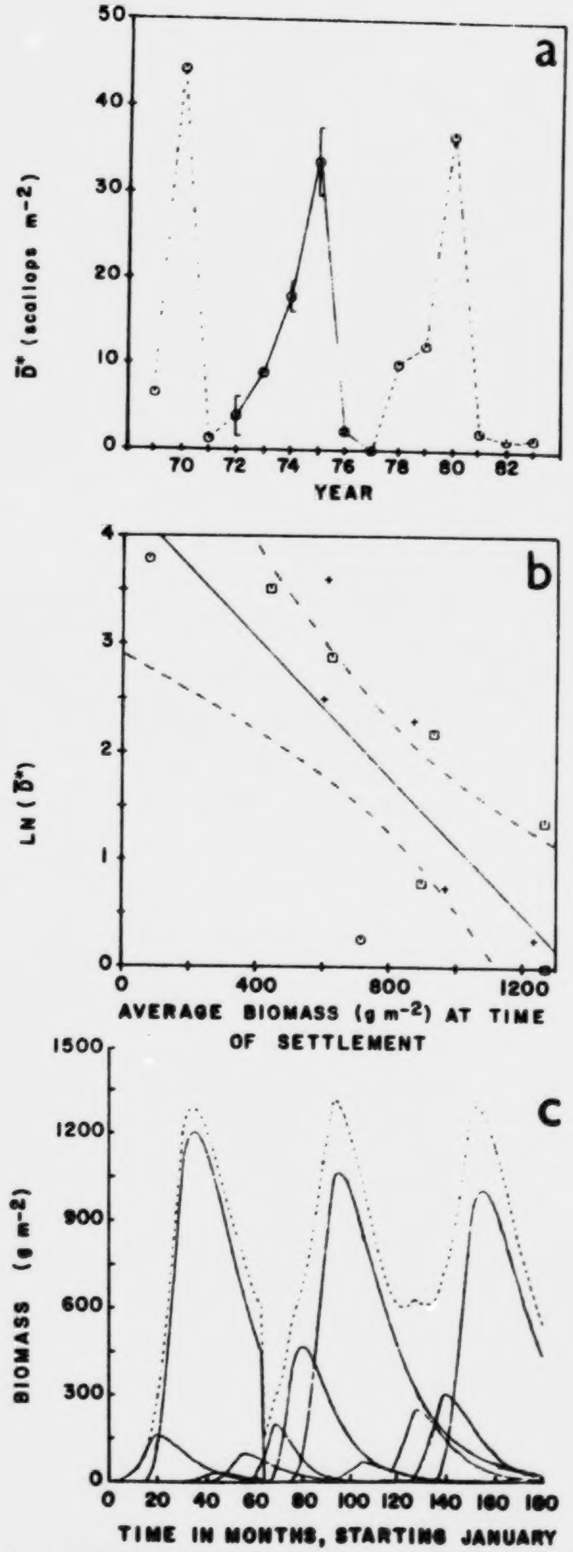

FIG. 12. Year-class strength and biomass, 1969–83. A: year class strength, as reflected by $\bar{D}^*$ (scallops·m^{-2}; 30 mm < $\bar{H}$ < 52 mm size); solid lines: years for which $\bar{D}^*$ was actually measured (vertical lines are 95% CL). B: log ($\bar{D}^*$) with regression and 95% CL, vs. average biomass at the time of settlement of each cohort; (○) backcalculated from *Sanjo-I* Survey (February 1973) data, (□) data from the 1974–78 study period, (+) from Ciocco, unpublished data (1978–82); C: Simulacrum results (see text) utilizing all existing information; dashed line: biomass (g·m^{-2}); solid lines: biomasses for each cohort (note the large 1970, 1975, and 1980 cohorts).

explained by several hypotheses, which can be broadly grouped into those involving exogenous and endogenous processes. I have been unable to identify any external factor explaining this pattern. In the following section I consider density-dependent recruitment, a potential endogenous mechanism.

4.3 Density-Dependence of Recruitment

When a year-class reaches age $t+$ (age at which $\bar{H} = 30$ mm, ~0.85 yr, early spring of the first year of life), its strength has already been modulated by factors that operate during early life history stages. Therefore, a time series of estimated average adult biomass values at the time that settlement peaks (January–February of each year) was assembled for the period 1970–83 for the San Román Ground high density area. Figure 12b shows log ($\bar{D}^*$) versus average adult biomass at the time of settlement.

A combination of high adult biomass at time of settlement and high $\bar{D}^*$ was never observed over the 14-yr study period. Year-class strength declines exponentially with increasing adult biomass at settlement; the negative correlation between log ($\bar{D}^*$ ind./m^2) and biomass (g·m^{-2}) at settlement is statistically significant ($r^2 = 0.596$, $N = 14$, $|0.05 < P < 0.01|$). The $\bar{D}^*_0$ ($\bar{D}^*$ expected for 0-Biomass) obtained from fitting a linear model is 76 scallops·m^{-2} (slope: -0.00317, intercept: 4.336). Weight of a 52 mm scallop (maximum size at $\bar{D}^*$) is ~15 g. Using growth and mortality parameters obtained from a robust cohort (1975), the expected $\bar{D}^*_0$ translates into a maximum biomass of ~1500 g·m^{-2}. This is the approximate carrying capacity according to other evidence (see below).

The following conceptual model is consistent with both the pattern disclosed by Fig. 12 and empirical/intuitive knowledge of the system:

1) A negative interaction (whose intimate nature is still not understood) exists between adult biomass and settlement (or recruitment to $\bar{H}+$). Settlement/recruitment is inhibited when biomass is above a threshold, which might be close to the upper confidence limit in Fig. 12b.

2) Settlement/recruitment at the within-ground scale may be successful even if adult densities are low (i.e., there is not a "descending" left hand limb in the stock-recruitment curve, as is the case in usual closed-stock models). The reason is that the depleted bed can be replenished by larvae from other grounds. This was the case following the catastrophic adult mortalities of 1973.

3) Even if there is "room" for settlement of a new cohort, this might fail for other reasons (e.g. climatic/hydrographic conditions).

Thus, using the frame of Fig. 12b as a graphic representation of this conceptual model, one expects to see some values in the lower-left half, but not towards the upper right. In other words, the probability of having a certain settlement level given some local adult biomass is split in two fields, separated by a "step" or "ridge" (roughly coincident with the represented upper dashed line). Above that boundary it is low. The shape of the probability density function below that boundary can not be determined from the few data available.

Existence of an adult–juvenile (or larval) interaction is suggested by spat settlement obtained from collectors suspended in midwater in the summers of 1976 and 1977, when substantial recruitment on the bottom was not observed (biomass was high in both years). Ruzzante and Zaixso (1984) quantified settlement on artificial collectors placed on the SW part of the gulf during the years 1978–82. Settlement always started in spring, and peaked in early-mid summer (January or February). The relative strength of settlement over the four periods studied by them, and of the subsequent strength of year-classes that settled on the San Román ground (N. Ciocco, pers. comm.) do not match:

settlement (SW): 1982 > 1980 ~ 1981 > 1979
year-class (SR): 1980 > 1979 > 1981 ~ 1982

That adult–juvenile interaction is not the sole factor behind the pattern is suggested because the 1976 year-class was poor all over the Gulf, whether adult biomass was locally high or low. By contrast, the 1975 year-class was generally robust all over the Gulf. In the San Román ground in particular, it was much stronger than would have been expected from simulation results. Synchronous relative strength of the 1975 and 1976 cohorts over the whole Gulf suggests factors homogeneously working over the entire area, at a scale above that at which adult–settlement interactions are relevant.

A negative interaction should be reflected in the spatial distribution of old and young scallops. Some evidence was extracted from an extensive survey done in June 1976, at a time when the age of the 1975 cohort was ~1.3 yr. Figure 13 shows a scatter of densities of 1+ (1975 cohort) vs. 2+ and older scallops in 146 quadrats (1-m^2) taken at random within different grounds. The important aspect displayed is that high densities of 1+ scallops were never coincident with high densities of older animals. The density range for 1+ scallops being 0–100, densities in the range 50–100 were always found at sites of very low adult density (0–10; the observed range of adult densities was 0–40). Maximum densities for "young" (1+) and "old" (2+ and older) scallops suggested that maximum carrying capacity was determined by biomass rather than by numbers, since

$$\max(\#\text{old})\ \bar{w}\ (\text{old}) = \max(\#\text{young})\ \bar{w}\ (\text{young})$$

where $\bar{w}$ is average individual weight. The dashed line of Fig. 13 can be seen as an approximate boundary of carrying capacity for both age groups combined. It corresponds to a biomass of ~1500 $g \cdot m^{-2}$, a figure consistent with results presented above.

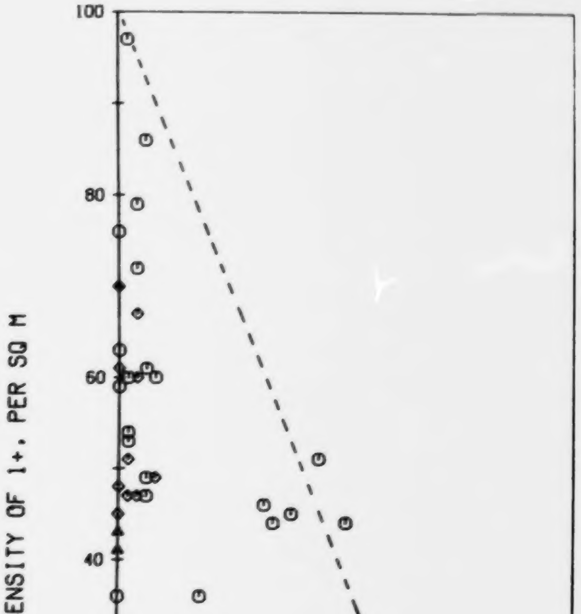

FIG. 13. Scallop density ($\text{scallops} \cdot m^{-2}$) at age 1+ (1975 cohort) plotted against the density of older scallops (May 1976). (○) Esfinge, San Román and Abanicos, (×) Tehuelche, (□) Conos, (◇) Iriarte-Ite. Notable.

5. BIOMASS AND PRODUCTION

5.1 Biomass

A computer "simulacrum" (Cushing 1982) was run starting January 1969. Estimated $\bar{D}^*$ values obtained above were used as the cohort's 'N_0s'. The bias of assuming that this was also each cohort's abundance over the age interval |0–0.85 yr| is irrelevant, as scallops are very small at this age. Growth and mortality parameters were as follows: cohort-specific for the year-classes 1973–75, average for the cohorts 1971–72, 1976–79, and 1981–83, and those estimated for the 1975 cohort were applied to the 1970 and 1980 cohorts (strong year-classes). A single, average length:weight relationship was used for all cohorts and all seasons. This simulacrum does not constitute a simulation, but simply a way to present a large amount of information in a compact format, and to estimate some missing biomass figures by interpolation.

Figure 14 shows observed biomasses ($g \cdot m^{-2}$) per date, and the average biomass trajectory generated by

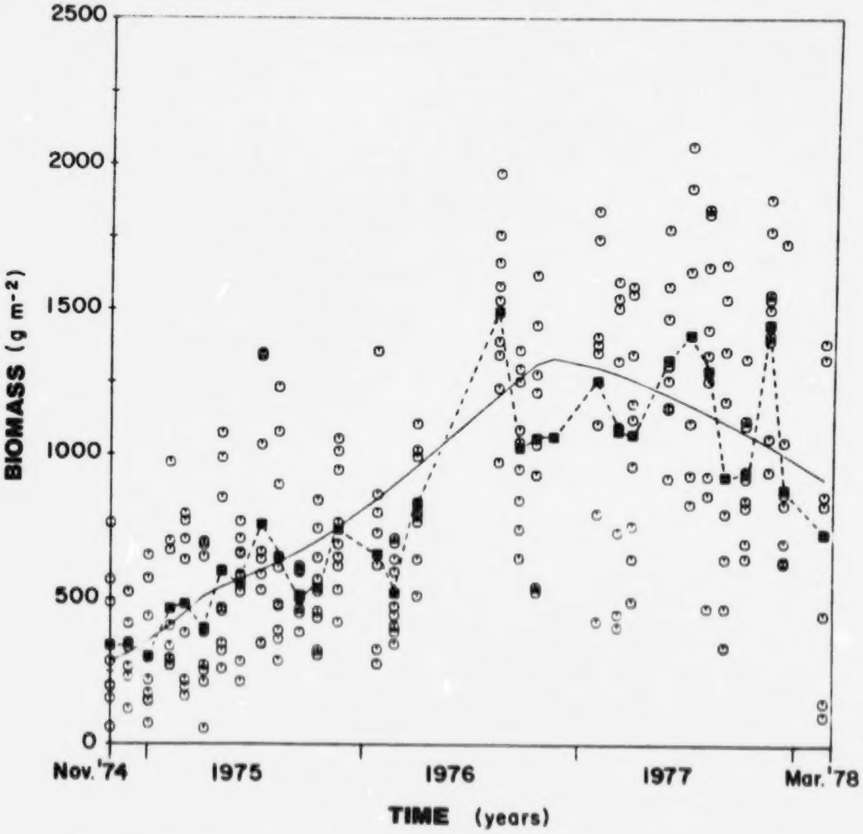

FIG. 14. Biomass (g·m⁻²) during the study period, Nov. 1974 through March, 1978. (○) individual measurements, (■) and dashed line: observed averages, solid line: trajectory generated with simulacrum.

the simulacrum for the period Nov. 1974–Jan. 1978. Deviates of observed average biomasses with respect to the model are in part due to the fact that a single length:weight relationship was used. Figure 12c shows the result of running the simulacrum from early 1969 to early 1984. The sharp drop of the 1970-cohort biomass (and consequently of total biomass) reflects the strandings of 1973, somewhat artificially introduced as a pulse in absence of detailed information on their exact timing.

When all the information was pieced together, the most interesting emergent feature was the apparent regularity of the total average biomass cycle, with maxima of about 1300 $g \cdot m^{-2}$ attained every 5 yr. This is consistent with results showing compensatory mechanisms above an average biomass of ~1000 $g \cdot m^{-2}$ (Results 2.3.2), and an upper boundary for biomass of ~1500 $g \cdot m^{-2}$ (Results 4.3).

To simulate essential aspects of behavior of the system, and of our target variables (average total biomass and relative year-class strength, expressed by $\bar{D}^*$), we used the difference equations for density dependent growth rate (Results: 2.3.3) and size-dependent mortality (Results: 3.2.1), and density-dependent recruitment pulses (Results: 4.3). Initial conditions were those found when this study started, in November–December 1974. The time increment for each step was one day. Projections were made for a 9-yr period. This allowed use of data for the years 1979–83 (N. Ciocco, unpubl. data) for validation (parameters in the equations were estimated with 1974–77 data). In each run parameter values were sampled from their respective distributions. This was used as a practical way to identify deviations in the system from its expected behavior. It would have been expected that a much stronger year class settled in 1979; a strong year class was not recruited until the following year. Exploration of relationships between these "anomalies" and "external" factors will be the subject of a forthcoming study.

5.2 Production

Production for the San Román Ground core bed was estimated by the "increment summation" method (Newman and Martin 1983; see Orensanz et al. 1985, for detailed figures). Annual production (P), average biomass ($\bar{B}$), and turnover (T) for two annual periods, |Nov.1974–Nov.1975| and |Nov.1975–Nov.1976|, are summarized below (standard errors in parenthesis):

	Nov.1974– Nov.1975	Nov.1975– Nov.1976
$\hat{P}$ ($g \cdot m^{-2}$)	761.78 (41.18)	766.76 (66.43)
$\bar{B}$ ($g \cdot m^{-2}$)	521.35 (10.64)	980.03 (23.44)
$\hat{T}$ (dimensionless)	1.46 (0.084)	0.78 (0.070)

The ratio shell weight/meat weight is close to 1 in San Román scallops (Results: 2.5). Using the estimated annual production figures above, average scallop meat production was 382 $g \cdot m^{-2} \cdot yr^{-1}$.

It is remarkable that although biomass almost doubled $\hat{P}$ stayed virtually the same. Turnover, correspondingly, dropped to one half. Turnover declined with age/size during ontogeny (Fig. 15b).

Vahl (1981a) showed very little change in net growth efficiency (NGE) during the first 5 years of life in a population of *Chlamys islandica*. Banse (1979) and Humphreys (1979) found no correlation between NGE and body size when invertebrate populations are compared over a broad range of body sizes. Thus, although age and size structure of the scallop population was not exactly the same in the 2 years, the amount of assimilated material was probably similar for both, as average NGE is not expected to have differed very much.

Negative production was observed as a result of seasonal changes in individual growth rate (Fig. 15a). There were three drops in weight in the year, corresponding to two spawning peaks and winter. When the 2 years are compared, the drops are more marked for equivalent groups during the high biomass year. Growth in weight was often (always during the high density year) negative during these minima for the 1+ and older year-classes.

6. HARVESTING

6.1 Commercial Size

Since 1971, legal commercial height for the tehuelche scallop has been 60 mm. Figure 16a illustrates recruitment of the 1973–76 cohorts. Practical effects of density-dependent growth are illustrated here by the contrast between the two cohorts which were most closely followed:

Cohort	Age (50% recruitment)	Experienced density conditions
1974	~1.5 yr	low
1975	~2.2 yr	high

Although originally established for different reasons, 60 mm turned out to be a reasonable, economic choice:

1) Maximum cohort biomass was observed shortly before 50% of the cohort reached 60 mm (Fig. 16b). Maximal values and fluctuations in total weight, total meat weight, and muscle weight are synchronous.

2) Average adductor muscle weight entered the smallest marketable size about two weeks after a size of 60 mm was reached, for all cohorts studied.

All criteria explored (average muscle size, muscle quality, recruitment to commercial size, maximum biomass) indicate that an average cohort should be ideally harvested during its second winter-spring for its yield to be maximized.

6.2 Harvesting techniques

Three methods of harvesting have been used in the San José Gulf: harvest of strandings, dredging, and commercial diving. Harvest of strandings does not present a real management problem. Dredging has been dealt with elsewhere (Orensanz et al. 1985; Vacas et al. 1984). Below I present some information on the diving fishery.

Divers search for and concentrate their fishing on highest density areas of the grounds (beds or "nucleos"). Once a good bed is found, a crew normally spends the whole working day on it. I estimated that the area in which a standard crew (5–7 divers) effectively operates over one working day ranges from 1 000 to 2 500 square metres.

In an experiment on June 24, 1977, a crew of 5 divers obtained a catch of 50 925 scallops. Density of the har-

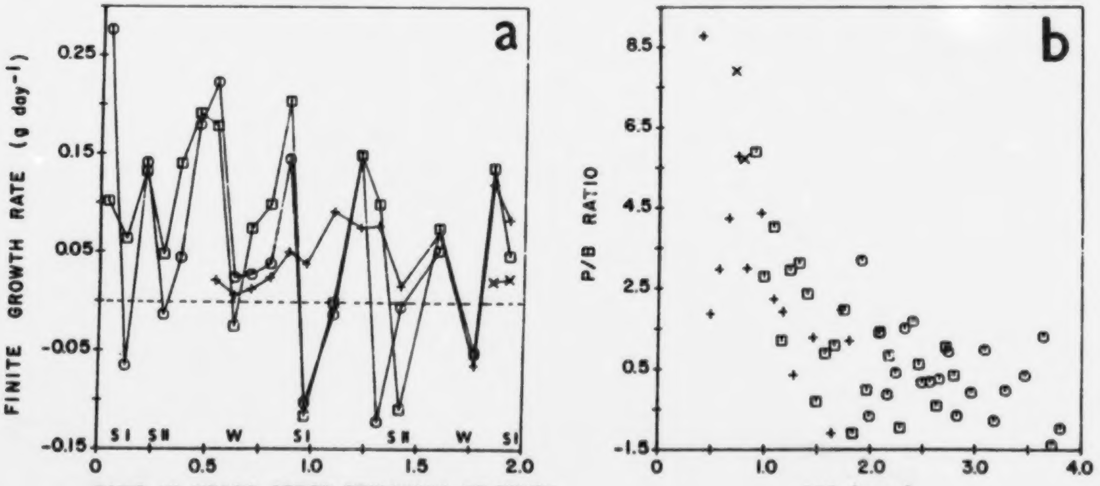

FIG. 15. (a) Finite weight growth rates ($g \cdot d^{-1}$) for the period Nov.1974–Nov.1976; SI and SII: spawning peaks, W: winter; (b) Annual Production/Average Biomass ratio plotted against scallop age; (○) 1973, (□) 1974, (+) 1975 cohorts.

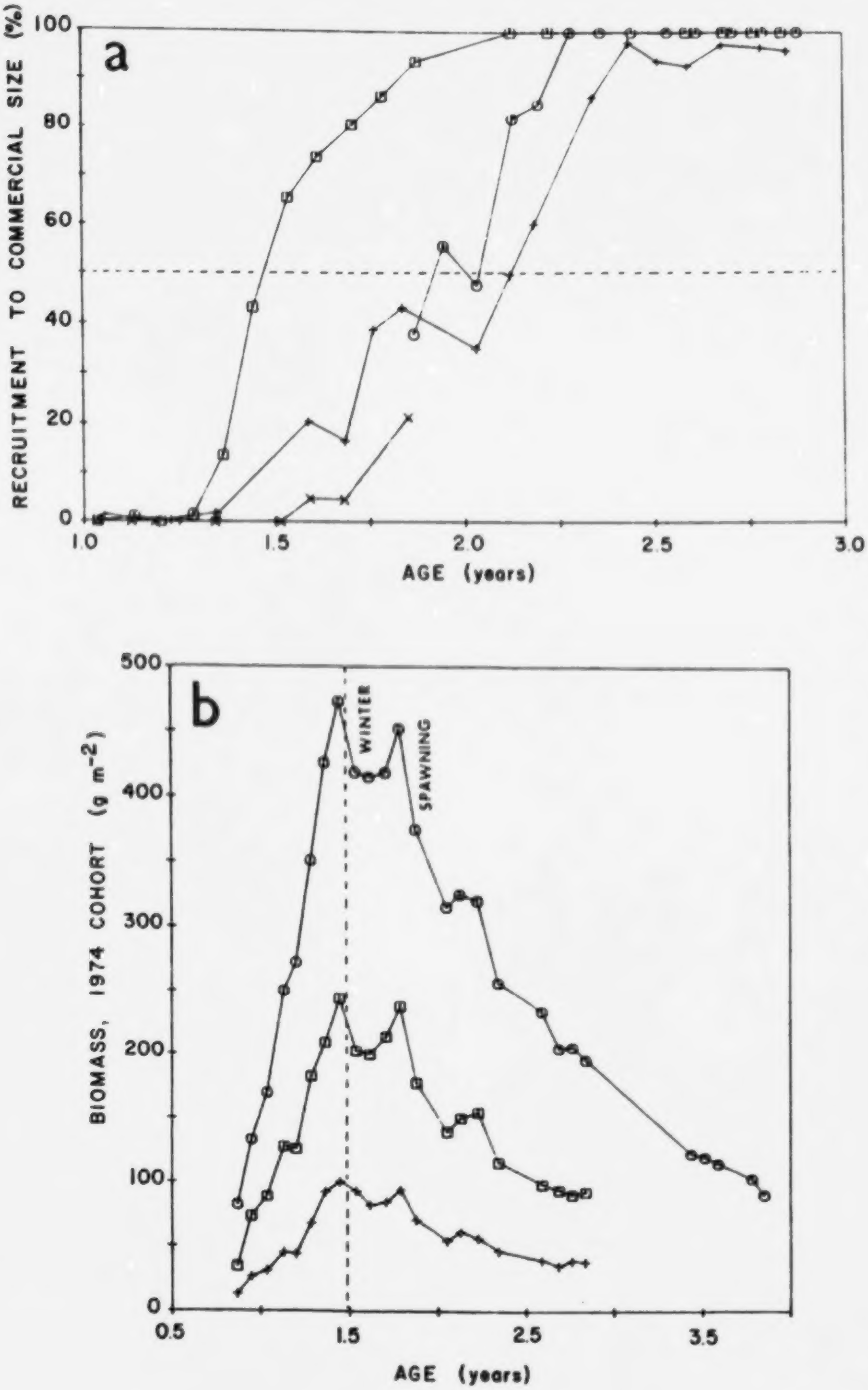

FIG. 16. Cohort recruitment and biomass. (a) Cohort recruitment to commercial size: percent of scallops, height > 60 mm, in monthly samples. Cohorts: (○) 1973, (□) 1974, (+) 1975, (×) 1976. (b) Biomass ($g \cdot m^{-2}$) of the 1974 cohort as a function of age by tissue type; (○) total weight, (□) soft tissue, (+) muscle; dashed line: age when size reached 60 mm.

vested bed was sampled by simple random sampling (0.25 square metre quadrats) before and after fishing, with the following results:

	Density (scallops·m^{-2})	SD	N
Before	60.4	20.5	46
After	42.0	21.9	43

showing a density drop of about 30% over the whole patch.

Out of 50 consecutive days over which a crew was followed in 1977, there were 24 effective working days. The best unit of effort seems to be the diver day. The following average CPUE (kg·diver^{-1}·d^{-1}, total weight) were measured:

Ground	Year	# of divers	# of effective working days	CPUE	Average density scallops·m^{-2}
San Román	1973	4–7	12	525	40
Iriarte	1977	5	24	450	50

These data show that in both periods (1973 and 1977) divers chose beds with very high average densities (40–60 scallops·m^{-2}). They were never seen fishing on beds with average densities below 20 scallops·m^{-2} (Fig. 3e).

Discussion

Results suggest that individual size, environment (geographic gradients and seasonal cycles) and density substantially influence the dynamics of the San José tehuelche scallop stock. Size influences both growth rate and stranding mortality. Environmental factors (temperature, food availability, storms) underlie seasonal fluctuations and between-ground contrasts. High density depresses condition, growth rate and reproductive output, presumably by reducing a limited food supply, and increases the risk of mortality from physiological stress. Figure 2 summarizes the interactive network. The discussion below follows the sequence outlined above. Three scales (L:large, M:meso, S:small) are conceptually defined in Tables 2 and 3, which also summarize questions of perception, representation and important biological attributes or implications. This hierarchy of scales is used to define the domains within which specific processes are assumed to operate homogeneously.

1. SIZE

1.1 Growth Rate

Over its first 1.5 yr of life and at moderate density levels, growth of *C. tehuelcha* can be reasonably well represented by a linear model (constant growth rate) plus a seasonal component related to both reproductive cycle (thus indirectly to temperature) and food availability (Results: 2.1). A declining trend in growth rate becomes perceptible after the second winter. It is common usage in fisheries biology to represent growth patterns of this type with asymptotic growth curves. While acknowledging the lack of phenomenological meaning of the parameters and other criticisms (Knight 1968; Roff 1980), such models are useful in presenting results in a succinct way, and in comparing growth between cohorts and between grounds (Results: 2.2).

Models where growth rate is an age-independent function of size alone (Equations 1,2,5) imply the potential for compensatory growth. The question has been addressed in clams (Eldridge and Eversole 1982) and bay scallops (Auster and Stewart 1984). Increased growth rate following the 1977 biomass decline seems to indicate such a potential for the tehuelche scallop. Reproductive potential has also been shown to be size — rather than age — dependent in at least one bivalve species (Peterson 1982). Although it is reasonable to assume potential for growth compensation ("catch up") within a moderate age range, an eventual age-dependent decline (senility effect) should not be disregarded.

1.2 Mortality

Natural mortality in the San Román sub-stock has a minimum value within the size range $30 < \bar{H} < 52$ mm (Results: 3.2.1). A monotonic increase in adult natural mortality with size/age has been also found in the european scallop (Gruffydd 1974a). Reviews of bivalve mortality patterns list other cases of sigmoidal survival curves (Hallam 1967; Cerrato 1980: fig. 24). Mortality minima at an intermediate age/size interval may be related, at least in some cases, to a transition in susceptibility to different sets of mortality sources, as is the case in the San Román population. Mortality sources with inverted size-dependence have been reported by Peterson (1982) for *Protothaca*.

2. ENVIRONMENT

2.1 Changes over time

Growth rate seasonality in natural populations of pectinids from temperate seas has been related to temperature (Kirby-Smith and Barber 1974), to fluctuations in the sestonic biomass (Ansell 1974; Broom and Mason 1978; Robinson et al. 1981), and to the relative proportions of suspended particulate organic and inorganic matter (Vahl 1980). In the San Román population somatic growth is primarily related to food availability (Results 2.1), with temperature playing a secondary role. Temperature was shown to be the primary factor for *Aequipecten irradians* in the Beaufort area (Kirby-Smith and Barber 1974), but water temperature range in that area (5–30°C) is much wider than in our case (9–17°C). Gonadal development is presumably related to temperature, as has been shown in other pectinids (Sastry 1968, 1979; Sastry and Blake 1971).

Relative growth of "storage organs" (adductor muscle, digestive gland, and to some extent the gonad) and reproductive materials shows a variety of patterns in pectinids. Differences between species and populations are mostly due to the relative timing of gametogenesis and reserve storage buildup. Usually there is a winter minimum for both. In some cases gametogenesis starts early in the winter, reserve materials are diverted to sustain it, and spawning takes place during early/mid-summer (number and timing of spawning peaks is very variable). That is the case for *Placopecten magellanicus* (Robinson et al. 1981), *Chlamys opercularis* (Taylor and Venn 1979), and *Pecten maximus* (Comely 1974). In *C. septemradiata* the main period of gonadal growth is spring, and the main spawning peak is delayed until late summer: in this species resources utilized for gonadal growth seem to come directly from the food being consumed (Ansell 1974). In the tehuelche scallop from San Román (Results 2.5) the muscle grew rapidly during the fall, and the gonad during late-winter/early-spring of 1974, suggesting that energy from food was sequentially diverted to reserve storage (fall) and gonadal maturation (spring). Other seasonal changes seemed to occur in phase, i.e., the relative weights of the different fractions are not negatively correlated. For example, both weight of the muscle and the "other meats" (which include the digestive gland) dropped synchronously with the gonad during spawning. This occurred for all year-classes and for all spawning peaks detected. A similar post-spawning general carbon loss was found by Barber and Blake (1985) in a bay scallop population. In tehuelche and tasmanian (Fairbridge 1953) scallops this results in a loss of consistency of the muscle, and a reduction of commercial value.

The utilization pattern of stored reserves in gametogenesis varies even intraspecifically. Barber and Blake (1983) hypothesized that utilization of reserves stored in the adductor muscle of bay scallops during gametogenesis increases with decreasing food supply along a latitudinal gradient. In the San Román tehuelche scallop population there were differences between the two years over which fractional weights were measured. During 1975 (high-biomass), there was no period of fast muscle growth.

In-situ mortality peaks (Results 3.2.2) were observed following minima in condition index (late winter/early spring: minimum food availability and temperature; post-spawning). Post-spawning deterioration in condition and increased mortality have also been reported for a bay scallop population (Barber and Blake 1983).

Growth rate depression was also shown to enhance *Polydora* infection (Results: 2.6), implying the possibility of a positive feedback loop of deterioration, since heavy infection leads to poor condition (Kent 1979). A similar relationship between decreasing growth rate and infection by shell borers has been observed in the Devonian *Paraspirifer–Vermiforichnus* interaction (Hoare and Walden 1983).

2.2 Gradients in Space

2.2.1 Utilization of nutrients by primary producers and the structure of benthic assemblages — Nitrates were a limiting factor for phytoplankton production in the Gulf (Charpy et al. 1980a,b,c; Charpy-Roubaud et al. 1978, 1983).

Three parallel NW–SE oriented gradients have been mentioned (Results 2.4):

a) environmental: temperature, density, nitrates (the last decreasing from NW to SE);

b) scallop growth rate declining from NW to SE; and

c) species dominance in sublittoral seaweed beds, shifting from *Ulva* in the NW to *Codium* in the SE.

The connection between the first two prompts an obvious explanation (Results 2.4). Is there a plausible linkage with the third?

It is hypothesized here that the gradient in algal dominance in the San José Gulf is related to the gradient of biologically available nitrogen. There is evidence suggesting that some forms of *Codium* are able to thrive in nitrate-limited environments. Head and Carpenter (1975), Dromgoole et al. (1978), and Rosenberg and Paerl (1981) have reported the association between nitrogen-fixing blue-green algae and bacteria, and species of *Codium*. The last authors showed that low levels of biologically available nitrogen were a limiting factor for algal growth in estuarine waters of the Beaufort area (North Carolina), and that a *Codium* species associated with symbiotic cyanophytes was abundant in relation to others which did not show that association.

A partition of the limited nitrate supply among primary producers (the phytoplankton, *Ulva*, *Codium*) might then be an important driving factor of benthic community structure and bivalve population dynamics, determining:

a) growth rate of suspension feeding bivalves, with all its implications for demographic schedules;

b) distribution of different algal bed types and their associated biota;

c) recruitment of scallops, for which *Ulva* is a main natural primary settlement substrate.

Several aspects of bentho-pelagic coupling have received attention in recent years. Structural and dynamic consequences of the nutrient utilization pattern suggested here would imply a novel type of interaction. I have observed similar distributional gradients of benthic algae in the adjacent San Matías and Nuevo Gulfs (unpubl. data).

2.2.2 Contrasts in mortality sources and their implications — Differences in prevalent mortality factors (Results: 1.1, 3.1) and survival patterns emerge when grounds are compared. Exposure to stranding seems to be the main factor. In exposed areas longevity is lower, empty shells contribute little to bottom sediments, shells show a smaller epibiont load (Results: 2.5, 3.2.3), and predators are scarcer.

Strandings can occasionally reach catastrophic proportions. Massive mortalities are not rare in scallop populations elsewhere, and have been observed as a result of massive predation (Brun 1968), disease (Marti et al. 1982), high temperatures (Dickie and Medcof 1963), freshwater runoff (Tettlebach et al. 1985), extremely cold winters (Ursin 1956; Crisp 1964), and stranding (Kalashnikov 1984). Stranding has also been reported as a source of massive mortality for other bivalves (Eggleston and Hickman 1972; Gruet 1983). More than a nuisance for parameter estimation, large mortality pulses are a fundamental aspect to be considered in scallop population dynamics. Their detection may be more important than estimation of constant mortality coefficients.

One possible reason for the observed scarcity of predators in exposed areas is that they too are exposed to stranding, and their recovery time may be longer. This might be the case for volutid gastropods, which propagate through encapsulated eggs without a pelagic phase (Penchaszadeh and De Mahieu 1976).

In general, epibionts seem to enhance survival of epibenthic bivalves. Vance (1978), Bloom (1975), and Forester (1979) found that fouling organisms reduce predation in chamid clams and scallops, and defined the association as a form of protective mutualism. Association between the tehuelche scallop and a monaxonid sponge resembles similar partnerships reported for *C. varia* (Forester 1979), *C. hastata hericia*, and *C. rubida* (Bloom 1975). Scallops do not seem to compete with their suspension feeding epibionts. A. Parma (pers. com.) found no correlation between different indices of condition and epibiontic load (composed mostly of barnacles and mussels) in samples from the San Matías Gulf, although the epibionts amounted to twice the weight of the scallops themselves.

In areas exposed to stranding, however, indirect evidence indicates that mortality increases with epibiontic load (Results 3.2.3). A similar situation was reported by Witman and Suchanek (1984) for mussels: individuals overgrown by kelp encountered flow-induced forces 2–6 times greater than did clean mussels, and epizoans increased the risk of dislodgement in an exposed beach.

The divergent effects of epibiosis described in the two preceeding paragraphs illustrate the workings of alternative sets of mortality sources and selective pressures, suggesting further avenues of inquiry. While the San José megapopulation is a mixture of stranding-exposed and non-exposed grounds, stranding has never been reported in the NW of the San Matías Gulf (Fig.1 b), where predation is a major source of mortality. One might expect selective pressures favoring a more "sedentary" outline (proportionally higher shells, more asymmetric auricles: Gould 1971; Stanley 1970, 1972) in San José. A preliminary analysis[2] showed that, indeed, the height:length relationship differs significantly between these populations, and has diverged as predicted by theory and as inferred from observed prevalent mortality sources. Kelley (1983) found that shell morphometric relationships differentiate within-species geographic populations in the Miocene genus *Chesapecten*, in contrast with what happens in several infaunal genera, and coincidently with what has been incidentally reported for other pectinids (Gould 1971; Fairbridge 1953). Regional variation in the balance between antagonistic selective pressures suggested here for the tehuelche scallop may help to understand the gradualistic made for the evolution of shape in scallop lineages. Selective pressures affecting shell shape seem more labile for epibenthic scallops than for infaunal clams.

3. DENSITY

3.1 Spatial Distribution Pattern

Although pattern descriptions based on quadrat-density distributions are useful for some practical purposes (Results: 1.2), they are more informative on attributes of quadrats than on attributes of organisms; inference on the latter is indirect and often inconclusive. Some concepts have to be defined to extract biological meaning from quadrat data.

While dealing with bivalve spatial processes we are concerned with 'ambits' (Lloyd 1967) or neighborhoods (Weiner 1982). Different types of these can be recognized:

- trophic, within which resources may be depleted,
- reproductive, related to gamete dilution away from the individual,
- sensory, within which emitted signals will be perceived, etc.

One square metre (the size of our sampling unit) is likely to be commensurate with adult scallop neighborhoods. So, we can use the number of scallops in a single sampling unit as a coarse approximation to neighborhood density experienced by each of those individual scallops.

Little attention has been paid in the literature to the distribution of individuals by neighborhood density levels, when compared with the number of studies dealing with quadrat density frequency distributions. Results on the tehuelche scallop (Fig. 3e; Results: 1.2) show that most animals experience rather high neighborhood densities. This simple result has important implications since compensatory mechanisms are expected to be relevant only in dense assemblages. Allen and Cranfield (1979) showed similar results for an oyster stock from New Zealand: 90% of individuals lived in high density beds. Density-dependent processes can be important even if they take place over small but densely populated areas.

3.2 Individual Growth and Condition

Several pieces of evidence suggest density-dependent growth in the San Román scallop ground (Results: 2.3). Density-dependent growth in benthic suspension-feeders is frequently attributed to intraspecific competition for food (Fréchette and Bourget 1985b). This implies that the resource in question is in short supply, and that its level can be effectively reduced in the neighborhood of an individual. Evidence of this is fragmentary. Seston depletion by suspension feeders has been shown or advocated for:

a) the neighborhood of individuals or clusters of individuals in still water (Bayne et al. 1976; Foster-Smith 1975);

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[2] I compared the height:length relationship between large samples from both stocks (# San José: 718, # San Matías: 1378; size range: 12–74 mm height for both samples). Covariance analysis with log-transformed measurements showed that scallops from San José have on the average proportionally higher shells [F(factors) = 182, d.f. = 1,2092; difference between slopes for the two areas was NS]. To give a feeling of the degree of divergence, the height/length ratio is predicted to be equal to 1 at $H = 47.50$ mm in San José, and at $H = 37.25$ mm in San Matías.

b) water flowing over suspension-feeding assemblages, either experimental (Buss and Jackson 1981; Wildish and Kristmanson 1984) or natural (Glynn 1973; Carlson et al. 1984; Fréchette and Bourget 1985a);

c) whole natural water bodies (Cloern 1982; Officer et al. 1982).

Another line of evidence is based on observations of an inverse relation between density and growth rate. Depressed growth under experimentally increased densities has been documented in oysters (Sheldon 1968), mussels (Stiven and Kuenzler 1979), cockles (Hancock 1966), clams (Ohba 1956; Eldridge et al. 1979; Jeng and Tyan 1982; Kline 1983; Peterson 1982), bay scallops (Duggan 1972), and rock scallops (Monical 1980). There is also field evidence of density-dependent growth for cockles (Brock 1980; Cole 1956; Ivell 1981; Sutherland 1982), razor clams (Tegelberg and Magoon 1969), clams (Hall 1983), and scallops (Gruffydd 1974b; Cooper and Marshall 1963).

This fragmentary evidence of competition coexists with the widespread intuitive feeling, in part shaped as a hypothesis by Levinton (1972), that planktonic resources are so unpredictable that compensatory regulation of suspension feeders' growth and survival is unlikely, and that variability in population size of suspension-feeding bivalves reflects the chaotic nature of their food supply. Two arguments counteract this feeling:

a) depleted food levels in the vicinity of the seafloor may be re-established with lags longer than suggested by our intuitive conception of an 'unpredictable, uncontrollable' suspended resource (Wildish and Peer 1983; Wildish and Kristmanson 1984). Also, horizontal advection near the bottom and vertical mixing can dilute, or locally erase, effects of resource depletion, implying that competitive interactions may be effective at rather large spatial scales. In other words, the trophic neighborhood of a competing individual tends to increase in association with horizontal advection near the sea floor. This by no means implies that competition effects vanish, but rather that neighborhoods widely overlap, making competition undetectable at some scales of observation. Experimental work along these lines is scarce: Kirby-Smith (1972) showed food depletion in a simplified unidirectional sequence of neighborhoods. To my knowledge, Hall (1983) presented the only attempt of quantification of suspension-feeding bivalve neighborhoods in a natural population. In scallops, the blurring of competitive effects should be maximal because of the additional effects of movement by the animals. This complicates the feasibility of small scale experiments, as conditions in a particular site might well reflect the average condition over a much wider domain.

b) Not all resources harvested by benthic suspension feeders are of pelagic origin. As foreseen by Levinton (1972) there is increasing evidence that the benthic microflora and deposited detrital materials and their associated bacteria may play an important role (Pratt and Campbell 1956; Davis and Marshall 1961; Vernet 1977; Peterson 1982). Peterson (1982) found a higher density-dependence in growth in *Protothaca*, largely feeding on benthic algae, than in *Chione*, a plankton feeder. Benthic microscopic algae constitute the main part of the diet of the tehuelche scallop (Vernet 1977).

Conditions for resource depletion and density-dependent growth will be met only in densely populated beds, but may be relevant if a large part of the stock is concentrated there. Unfortunately, many studies on bivalve growth and dynamics are in sparsely populated areas, with no information on the general structure of the corresponding megapopulations.

3.3 Reproduction

Reproductive output was depressed as a result of density-dependent effects (Results: 2.3.4) before growth rate was affected (Results 2.3.2). It is difficult to determine whether this results in an effective reduction of the number of gametes fertilized per capita, since fertilization rate may be expected to increase with density (Pennington 1984). If the latter is the predominant factor, removal of the densest segments of the stock may have a disproportionate effect on a population's reproductive success (Gross and Smyth 1946; Fairbridge 1953). This may be an important problem with harvest techniques that, as commercial diving can efficiently locate and deplete the densest segments of the stock.

3.4 Mortality

Growth and mortality are counterintuitively linked in the San Román ground. I presented evidence of increased mortality in cohorts which grew faster (Results 3.2.1), and indirect evidence (Results: 3.2.3) of intracohort, size-dependent, differential mortality. However, if poor condition results in pulses of in-situ mortality over periods of increased stress (Results: 3.2.2), then mortality might sometimes increase at higher densities, when condition is already poor.

Growth depression is a more proximal effect of density-dependent starvation than is increased mortality. It is reasonable, then, to expect that the first will be observed more often than the second. Density-dependent mortality attributable to starvation has been shown in clams by Ohba (1956), but not in oysters (Sheldon 1968) or other clam studies (Eldridge et al. 1979; Jeng and Tyan 1982; Peterson 1982). The hierarchy of effects proposed by Peterson (1982) for *Protothaca* and *Chione*: perception> emigration> reproductive effort> growth> survival, applies as well to the San Román scallop population.

3.5 Settlement/Recruitment

Density-dependent recruitment emerged as the potentially most powerful regulatory mechanism (Results: 4.3), and also the most difficult to study. Adult-larval interactions have been the subject of much speculation (Thorson 1966; Mileikovsky 1974; Woodin 1976). A negative relationship between adult density and recruitment in suspension feeding bivalves has been observed in field populations of cockles (Kristensen 1957; Hancock 1973; Brock 1980), razor clams (Tegelberg and Magoon 1969) and scallops (Vahl 1982; this study), and in experimental density manipulations involving clams (Williams 1980; Peterson 1982). It is unclear whether the main inhibitory effect involves pediveligers being inhaled by adults (Kristensen 1957), juveniles being out-competed by their older neighbors (Weinberg 1985), or intra-cohort self-thinning (Ohba 1956). Capacity to withstand periods of food shortage are likely to be lower in small/young (0+ age) bivalves, as compared to adults, since storage organs may be proportionally less efficient buffers.

Two factors contribute to the complexity of any postulated mechanism of negative adult-larval interaction:

a) refuge provided by primary settlement substrates. In mussels (Bayne 1964), scallops (Paul 1981), and even cockles (Labourg and Lasserre 1980), primary settlement in substrates elevated from the bottom (algae, bryozoans, hydrozoans, seagrasses) may alleviate negative interactions.

b) Existence of mechanisms for post-settlement dispersal (Baggerman 1953; Sigurdsson et al. 1976) which may result in different areas for settlement and recruitment (Vahl 1982).

The main primary settlement substrate in San José was *Ulva* (Results: 4.1), thus differing from San Matías where it is shell hash (Olivier and Capitoli 1980). Near-bottom masses of drifting unattached *Ulva* are a vehicle for passive spat redistribution over the grounds. Timing of seasonal *Ulva* blooms, interannual variation in distribution of algal beds, and large algal strandings may partially determine scallop year class strength.

No matter how important small to medium scale adult-larval/juvenile interactions may be, a large scale component, presumably related to hydrographic/climatic conditions, is also present. For the three years for which spawning schedule data are available (1974–76), the year where the spring spawning peak was most delayed (1974) resulted in the strongest cohort (1975). A relationship between year-class strength and pattern of temperature increase during the proliferation/spawning season was found by Yamamoto (1950) in the ezo scallop stock of Mutsu Bay. A similar mechanism might operate in this case.

3.6 Cycles

A 5-yr cycle of year-class strength and average biomass in the San Román ground dense core was detected for the 15-yr period 1969–83 (Results: 4.2, 5.1). The cycle was produced by three exceptionally strong year-classes (1970, 1975, 1980). Multi-year population cycles have been an important problem in population ecology. They can result from predator-prey interactions, non-linear renewal, or fluctuations in an external variable influencing recruitment. Multi-year cycles have been reported for other shellfish stocks (Caddy 1979; Botsford and Wickham 1979; Botsford 1982; McKelvey et al. 1980).

Whether the cycle reported here is a predictable phenomenon is not known. The observed recruitment pattern may have been the result of chance, or may reflect a cycle in a still unknown "external" variable. Although we have presented evidence of density-dependent recruitment, its exact underlying mechanisms are obscure. The cycle may be spurious for the following two reasons: (1) strength of the 1975 year-class was to some extent a feature common to all populations, and, if density-dependence really existed, it might well have been enhanced by storms in 1973–74; (2) in 1979 there seemed to be "enough room" in the ground for recruitment of a stronger cohort. Thus, even if density-dependence influences year class strength to some extent, the observed pattern was probably the result of its interaction with random or large-scale events. Caution is also advised in interpreting the regularity of average biomass maxima (Fig. 13c). They reflect the fact that carrying capacity was reached at the dense centre of the ground, but are only indirectly informative on the total size of the substock (lateral expansions and contractions are not accounted for).

3.7 Production

Convergence of annual production figures for 2 years with different average biomass (Results 5.2) is an indication that:

a) some sort of compensatory mechanism exists: although biomass almost doubled from one year to the next, annual production stayed the same;

b) effectively there is a carrying capacity;

c) carrying capacity was reached by the population during the course of the study (the amount of assimilated material was probably the same for both years; Results: 5.2).

Charpy-Roubaud et al. (1982) estimated that phytoplankton production at San Román ($161\ g\,C\cdot m^{-2}\cdot yr^{-1}$, resuspended microphytobenthos not discriminated) could support an annual production of $379\ g\cdot m^{-2}\cdot yr^{-1}$ of herbivore bivalve meats. Annual scallop meat production in Nov.1974–Nov.1976 ($382\ g\cdot m^{-2}\cdot yr^{-1}$) was virtually the same as the carrying capacity estimated independently by Charpy-Roubaud et al. This strengthens the suggestion that the dense core of the San Román population was at its carrying capacity in 1974–75, and that depressed growth in 1975 was the result of the increase in density. It also confirms the qualitative observation of the local monopoly of suspended resources by scallops; biomass of other benthic suspensivores was insignificant in the high density area, and zooplankton was always scarce (Charpy-Roubaud et al. 1978).

With filtration rates of the order of $1\text{-}L\cdot hr^{-1}\cdot g^{-1}$ of wet weight, which has been estimated for other temperate *Chlamys* species (Foster-Smith 1975), a dense patch of scallops (average biomass $= 1200\ g\cdot m^{-2}$ or more, or ~600 g of flesh$\cdot m^{-2}$, the approximate carrying capacity of the core) would filter a volume of about 14 400 L of water every day, which is equivalent to the overlying water column (~8 000–17 000 L).

3.8 Harvesting

Divers are efficient in focussing effort on the densest segments of the population (Results 6.2), and they stop fishing when density reaches a certain threshold value. This was above 20 scallops$\cdot m^{-2}$ during the study period, but I expect it to be a function of economic reward. This is an extreme case of density-dependent effort allocation (Caddy 1975), which suggests that the diving fishery has good potential for self-regulation.

4. IMPLICATIONS FOR FURTHER RESEARCH AND MANAGEMENT

4.1 Alternative Harvest Techniques

Unlike conventional fishing techniques, shellfish harvesting devices may have a great effect on the recovery of a harvested patch. Local recovery may be related to changes in substrate and structure of the benthic community rather than to the amount of the target species which is removed (Fonseca et al. 1984; Orensanz et al. 1985).

Much concern about the use of dredges in the fishery followed the collapse of the tehuelche scallop stocks of the NW of the San Matias Gulf in 1971. Olivier and Capitoli (1980) suggested that removal of thousands of tons of shell hash (the natural spat collector in that area) from the San Matias grounds in 1968–71 was responsible for several years of poor or no settlement (1971–79). Dredgers do not sort the catch aboard, and regulation of that activity is unlikely to be successfully implemented. Dredging has a major impact on benthic assemblages (Orensanz et al. 1985), has a low efficiency (around 14%; Vacas et al. 1985), and is often completely unselective as to size of scallop fished (Orensanz et al. 1985). Vacas et al. (1984) etimated that in heavily fished areas of the NW of the San Matias Gulf each site was dredged an average of 5 times during the 1983 fishing season. This implies a high level of disturbance, especially in view of the subtleties in structure and organization of marine benthic communities shown by current ecological research. Disturbance (Caddy 1973) and incidental damage and mortality (Gruffydd 1972; Merrill et al. 1961; Naidu 1982) have been reported for other dredging scallop fisheries as well. Similar concerns have led to banning dredges in various parts of the world. Long-term effects of fishing gear (Holme 1983), though difficult to detect, should receive more attention from applied ecologists.

Trawling is an alternative to dredging on smooth grounds, and to diving in deep waters. It has been employed in the calico scallop fishery off the SE United States. Our preliminary experimental results were encouraging. Experimental studies (Graham 1955; Gibbs et al. 1980) have shown it to be less deleterious than dredging.

Commercial diving (Results: 6.2) is a viable alternative for exploitation of shallow-water grounds. Commercial scallop diving has been used in Chile and Perú (*Aequipecten purpuratus*), the Gulf of California (*Pecten vogdesi*), and Great Britain (*Pecten maximus* and *Chlamys opercularis*; Hardy 1981). We found commercial diving to be highly selective (Orensanz et al. 1985) and non-disturbing. Diving fishermen soon develop a searching image for size, and select large scallops ($H>60$ mm height) for economic reasons (Results: 6.1), whether a minimum size is enforced or not.

4.2 Management Models and Suggestions for Future Research

Several types of models have been applied to exploited bivalve populations: non-renewable resource models (Cessine and Strand 1978), "yield per recruit" models (Mason et al. 1979; Serchuk et al. 1979) and their "pulse-fishing" situation version (Munch-Petersen 1973), "stock production" type models (Hughes and Bourne 1981; Fernandez Pato 1979), stock–recruitment relationships (Hancock 1973), linear age-structured models (Brousseau et al. 1982; Baglivo et al. 1982) based on demographic schedules (Brousseau 1978; Vahl 1981b), age-structure models with non-linear interactions (Conrad 1982), and computer simulations (Marchesseault et al. 1981; Caddy 1975).

Most of these models were developed with finfish resources in mind (Hancock 1979), and may be inadequate to deal with bivalve fisheries for some of the following reasons:

a) Bivalve stocks are contagiously distributed. Growth, mortality, fecundity and recruitment are subject to locally persistent spatial variation. Allocation of effort tends to match spatial pattern of the stock; sedentary habit precludes the horizontal compensation mechanisms (due to motility) which are advocated in dealing with fish (Caddy 1975; Jamieson 1978).

b) They are complex megapopulations, with open segments interconnected by larval dispersal. A depleted ground can be repopulated by larvae produced somewhere else. Relation between stock and recruitment, therefore, is the result of several processes which are decoupled because of their different temporal and spatial scales: on one side larval availability will depend on large-scale conditions (hydrographic variables, size of the whole stock), while site receptiveness to settlement will depend on small-scale conditions (Tables 2 and 3).

c) Self regulating mechanisms, although geographically restricted, may be locally important in bivalve populations. Non-linearities (mostly in renewal) cannot be dismissed in small-medium scale situations (within-ground, within-bed; Tables 2 and 3).

d) Recovery of a harvested patch may be more related to the impact of fishing gear on benthic communities than to the amount of the target species removed (Discussion: 4.1).

Managers usually try to maximize yield in a "sustainable" way. In the tehuelche scallop, harvestable beds are normally dominated by one strong year-class. Maximum biomass and commercial quality-standard criteria make it advisable to center the harvest of a single cohort around the second half of its second year of life (Results: 6). The diving fishery has the potential for self-regulation, as it concentrates on dense beds (Results 6.2, Discussion: 3.8) and selects commercial-size animals. Thus, the goal of maximizing the yield of recruited cohorts (growth overfishing problem) can be left to the fishermen. The main research/management concern with regard to the tehuelche scallop stock should be recruitment overfishing.

Bivalve stocks are conceived differently in the forelisted model types with regard to recruitment overfish-

TABLE 2. Scales of aggregation and scale-specific problems important in conceptualizing renewability of a scallop stock.

Scale	Investigated through	Usually represented by means of:	Aspect implied in stock renewability:	Life historical stage involved:
Large	Surveys of stock abundance and distribution	Distributional maps	Recovery of a depleted stock by imported dispersal stages	Pelagic larvae, through between-grounds dispersal
Meso	Inference from spatial distribution patterns	Density frequency distributions	Spatial dynamics of bed formation/dilution, as related to the density threshold levels for the harvesting technique	Adults, through displacements and aggregative/disaggregative behavioral or other mechanisms
Small	Experimental manipulation	Charts of individuals position; individual movement trajectories	Density-dependence of fertilization rate	Gamete broadcasts

TABLE 3. Intrinsic factors underlying within-ground scallop spatial distribution patterns.

Life history stage involved	Scale		Scenario	What is expected to be maximized:	How is it expected to be achieved:	Where is natural selection expected to operate:
	Time	Space				
Gametes, from spawning to fertilization	small (minutes)	small (cm)	Patch or site (neighborhood of an individual)	Fertilization rate	Spacing of reproductive adults	Density-dependence of threshold levels for movement triggers
Pelagic larva, from fertilization to settlement	Interm. (days)	large (km)	Region (megapopulation)	Early benthic survival	Selection of habitat	Searching behavior and cues triggering settlement
Benthic juveniles and adults, from settlement to death	Large (years)	Interm. (m)	Bed or ground (population)	Adult survival; net reproductive output	Selection of habitat	Cues (predators, environmental conditions) eliciting movement and their threshold levels

ing. First, they can be seen as either non-renewable (Cessine and Strand 1978) or renewable. If the latter, "renewability" may be a result of (a) the stock being supplied by constant recruitment (equilibrium "yield per recruit" models), (b) growing population size (linear renewal models), or (c) productivity being a nonlinear function of population size, this last whether the population is an amorphous biomass ("stock-production" models), semelparous ("stock-recruitment" models), or iteroparous and age-structured (non-linear renewal models).

The non-renewable resource problem is of no interest in our context. There is no indication that the San José stock is growing, nor that any of its segments are supplied by constant recruitment. The San José megapopulation may be "renewable" because of a mixture of (a) localized and sporadic recruitment pulses resulting in harvest opportunities, and (b) non-linearities in the renewal of populations.

In summary, the fishery described is a multiple pulse fishery with partially self-regulated populations interconnected by larval dispersal. Conventional management models cannot deal appropriately with renewability in such a situation. Analytic models are useful to handle single-scale problems (larval dispersal matrix, or within-ground dynamics), but a quantitative representation of the whole stock or of mixed-scale processes can be practically done only by means of computer simulation.

This stock offers the opportunity to implement a management and research program in which unproductive enforcement costs are replaced by a rewarding investment in information. The diving fishery (because of its self-regulatory potential) can be deregulated, although changes in the harvest threshold density should be closely monitored. Experimental dredging could be allowed in restricted areas, where the recovery of the scallop beds could be followed and compared with control closures and diver-harvested areas. Relevant experimental research questions that should complement management and modeling include the density-dependence of adult movements, fertilization rate, and settlement (all small-scale processes), the correlation between year-class strength and environmental factors, and the among-grounds larval dispersal pattern and rates (large-scale processes). The most relevant question relative to the diving fishery is to what extent a very selective removal of the densest beds has a disproportionate effect on recruitment (one of Gross and Smyth's largely overlooked hypotheses). The disturbance-dependence of dredged beds recovery (Olivier and Capitoli Hypothesis) is the most important question from the viewpoint of the dredging fishery).

The spatial structure dress of bivalve stocks presents difficulties which are seldom acknowledged in approaches patterned after the "finfish experience", but, from the viewpoint of researchers and managers, it also offers advantages which are, unfortunately, seldom exploited. Scattered in the shellfish literature are the elements for new conceptual models of shellfish population structure, closer to applied plant ecology than to finfish stock dynamics.

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Population Dynamics and Assessment of Exploited Invertebrate Stocks

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Methods for analyzing effects of exploitation on harvested populations have been primarily developed for vertebrates. Attempts to explicitly account for life history features of invertebrates are comparatively recent. We consider modifications to two broad classes of fishery assessment models, surplus production and dynamic pool models, with specific application to invertebrate populations.

Two delayed recruitment models are described and contrasted. Time delays are important in modeling invertebrate fisheries, since the lag between spawning and recruitment may be considerable. An extension of the Pella-Tomlinson generalized production model with time delayed recruitment is described. An alternative production modeling approach which attempts to explicitly model growth, recruitment and survival is also described. This model is defined in discrete time and time lags are easily incorporated. Unlike the above variant of the Pella–Tomlinson model, parameters of this model may be estimated independently of catch/effort data.

Modifications of dynamic pool models to allow for density dependent growth, environmental effects, and seasonal patterns of growth and mortality are also described. A yield-per-recruit analysis for sedentary, aggregated populations which allows for differential harvesting among sectors in a two-dimensional matrix, representing the area occupied by the stock, is described. The approach allows varying growth and natural mortality among sectors. Alternative harvesting strategies can be simulated for differing aggregation patterns and population parameter estimates. Applications of the model are illustrated for Atlantic surf clam, *Spisula solidissima*, stocks off the northeast USA. We also describe an analysis for a crustacean population which considers discontinuous growth patterns and seasonality in mortality rates.

Les méthodes permettant d'analyser les effets de l'exploitation sur les populations pêchées ont été mises au point en premier lieu pour les vertébrés. Les tentatives faites en vue d'expliciter les caractéristiques du cycle vital des invertébrés sont relativement récentes. Nous examinons les modifications apportées à deux grandes classes de modèles d'évaluation de la pêche, la production excédentaire et des modèles dynamiques de bassins, en les appliquant en particulier à des populations d'invertébrés.

On décrit deux modèles de recrutement retardé et on les compare. Les retards sont importants dans la modélisation des pêches d'invertébrés, puisque le décalage entre la fraye et le recrutement peut être considérable. On décrit un prolongement du modèle de production généralisé de Pella–Tomlinson avec recrutement retardé dans le temps. On décrit également une autre approche de modélisation de la production qui tente d'expliquer la croissance du modèle, le recrutement et la survie. Ce modèle est défini en temps discret et les décalages sont facilement intégrés. Contrairement à la variante susmentionnée du modèle de Pella-Tomlinson, on peut évaluer les paramètres de ce modèle indépendamment des données sur les prises et l'effort de pêche.

On décrit également des modifications de modèles dynamiques de bassins pour tenir compte de la croissance qui est fonction de la densité, des effets sur l'environnement et des modes saisonniers de croissance et de mortalité. On fait une analyse du rendement par recrue pour les populations sédentaires et réunies qui tient compte d'une exploitation différentielle entre les secteurs de pêche dans une matrice à deux dimensions, qui représente la zone occupée par le stock. Cette approche permet d'évaluer la variation de la croissance et de la mortalité naturelle entre les secteurs. On peut simuler d'autres stratégies d'exploitation pour différents modes de rassemblement et estimations de paramètres des populations. On illustre les applications du modèle pour les stocks de mactre d'Amérique, *Spisula solidissima*, qui se trouvent au large de la côte nord-est des É.-U. Nous faisons également une analyse d'une population de crustacés où nous examinons les modes de croissance discontinus et le caractère saisonnier des taux de mortalité.

Introduction

Classical developments in the theory of the dynamics of harvested populations have been primarily motivated by the study of vertebrates. Indeed, until recently, little attention was devoted to specialized invertebrate life history characteristics in development of assessment and management models, despite the considerable economic importance of this group. Hancock (1979) reviewed features of exploited invertebrates which require special consideration including difficulty in age determination, discontinuous growth of crustacea, marked density dependence in growth rates of sessile species, intensive seasonal fisheries, seasonal variation in catchability, and difficulty in effort standardization.

We describe modifications to two broad classes of standard fishery assessment methods, surplus production and dynamic pool models, to accommodate invertebrate life history characteristics. The importance of incorporating time delays in surplus production models is explored since a multi-year delay between spawning and recruitment to the fishery is characteristic of many invertebrate stocks. A modification of the Pella–Tomlinson (1969) generalized production model with time delayed recruitment is described. We also present simplified delay-difference population model (Deriso 1980; Schnute 1985) which is applicable to heavily exploited invertebrate fisheries.

Development of yield-per-recruit models for invertebrate stocks requires particular consideration of density dependent growth rates, variation in fishing mortality rates due to intense seasonal fisheries, and discontinuous and/or seasonal growth patterns. Modifications of the Thompson and Bell (1934) yield model to account for these factors are described with particular emphasis on developing harvesting strategies for sedentary mollusc populations characterized by density dependent growth. We also consider yield models for crustacean populations which incorporate discrete seasonal growth and mortality patterns.

The sequence of models described in this paper represents a continuum of increasingly detailed approaches to describing invertebrate population dynamics. Data requirements for models increase correspondingly. Development of delayed recruitment production models allows explicit representation of the recruitment process while retaining simple data requirements. In particular, information on age or size structure of the population is not required. Models of the form proposed by Deriso (1980) and Schnute (1985) allow further separation of individual components of production (growth, mortality, and recruitment) and are amenable to analysis with catch-effort data alone or with ancillary biological information. Both classes of models allow appropriate reproductive lags to be considered, a feature which is deemed necessary for an adequate description of population dynamics of many long lived invertebrate species. Yield-per-recruit models described herein allow detailed description of growth and mortality processes; however, data requirements increase markedly. The choice of modeling approaches will therefore be determined by the nature of available life history and fishery-related information.

Due to the difficulty in estimating growth and mortality rates in crustacean populations, considerable emphasis has been placed on use of surplus production models (Abramson and Tomlinson 1972; Marchesseault et al. 1976; Skuladottir 1979; Morgan 1979; Saila et al. 1979). Momot and Gowing (1977) provided an interesting experimental analysis of application of production models to a crayfish population. Abramson and Tomlinson (1972) and Francis (1980) concluded that use of these simple models holds considerable advantage for analysis of crustacean populations. In addition, extensive time series of catch and effort information are available for a number of crustaceans. In contrast, little comparable information is available for mollusc populations. We have drawn exclusively from crustacean populations to illustrate the use of production models, however, the principles apply equally to molluscs. Growth and mortality rates are more readily studied in mollusc populations and we present a detailed example of application of a yield per recruit model for a bivalve population.

Production Models

The dynamics of a closed, exploited population reflect the difference between losses in biomass due to natural and fishing mortality and increases due to recruitment and growth. Individual estimates of recruitment, growth and mortality rates may not be readily available. This will often be true in developing fisheries where intensive biological studies have not been conducted or where it is difficult or impossible to estimate these parameters. Harvesting models proposed by Schaefer (1954, 1957), Pella and Tomlinson (1969), Fox (1970), and Schnute (1977) do not attempt to distinguish among individual elements of production but rather model the dynamics of an exploited population using a compensatory population growth model such as the logistic (Schaefer 1954, 1957; Schnute 1977), Gompertz (Fox 1970), or Bernoulli (Pella and Tomlinson 1969) functions.

Limitations of this approach have been extensively reviewed (Ricker 1975; Sissenwine 1978; Gulland 1983). Among the principle objections to surplus production models is the assumption of no time delays in production processes. To counter this objection, addition of delay terms has been considered by Walter (1973) and Marchesseault et al. (1976). Another objection not easily corrected in the context of these models is the composite nature of the model parameters.

An alternative but more demanding modeling approach would explicitly include expressions for individual components of production. Models which incorporate recruitment and survival terms have been described by Clark (1976) and Beddington (1978). Deriso (1980) and Schnute (1985) describe models which also include a growth component.

A. Delay-Differential Model

We derive below a generalized production model with explicit consideration of time delayed recruitment:

$$(1)\quad \frac{dB}{dt} = aB_t - bB_t^m + G(B_{t-r}) - qf_tB_t$$

where B_t is population biomass at time t, a and b are model parameters, m is a shape parameter, q is the catchability coefficient, f_t is standardized fishing effort at time (t), and $G(B_{t-r})$ is a recruitment function reflecting the influence of spawning biomass lagged by r years. Model (1) is therefore a variant of the Pella–Tomlinson (1969) general production model with a discrete lag structure. In general, a closed form solution of the time delay model is not possible. For the simple case where recruitment rate is taken to be proportional to spawning stock (r) years earlier (i.e., density independent; Marchesseault et al. 1976) then $G(B_{t-r}) = cB_{t-r}$ where c is rate of recruitment per unit spawning biomass. This model is therefore a generalization of the model proposed by Marchesseault et al. (1976). For simplicity, we have assumed that spawning stock and exploitable biomass are identical, although this requirement is easily modified. Biomass at several past spawning stock sizes may be included if recruitment to the fishery occurs over several years. Noting that at equilibrium $B_t = B_{t-r}$, the biomass level at which yield in maximized (B^*) is given by:

$$(2) \quad B^* = \left(\frac{a + c}{mb}\right)^{\frac{1}{m-1}}$$

Maximum equilibrium yield, MEY, is then:

$$(3) \quad \text{MEY} = (a + c)\left(1 - \frac{1}{m}\right)\left(\frac{a + c}{mb}\right)^{\frac{1}{m-1}}$$

and the level of fishing effort at which yield is maximized (f^*) may be expressed:

$$(4) \quad f^* = \left[(a + c)\left(1 - \frac{1}{m}\right)\right]/q$$

The equilibrium relationship between yield and fishing effort is given by:

$$(5) \quad Y^* = qf\left[\frac{(a + c) - qf}{b}\right]^{\frac{1}{m-1}}$$

To express the model in terms of observable quantities and to provide a simple estimation procedure, we first note that:

$$(6) \quad \frac{1}{B}\frac{dB}{dt} = \frac{d(\ell n\ B)}{dt} = a - bB_t^{m-1} + c\,\frac{B_{t-r}}{B_t} - qf_t$$

and that a finite difference approximation to the relative derivative term with $\Delta t = 1$ yr is given by

$$(7) \quad \frac{1}{B}\frac{dB}{dt} \doteq \ell n\ (B_{t+1}/B_t)$$

Noting that $Y_t = qf_tB_t$ and substituting U_t/q for B_t where U_t is the catch-per-unit-effort (Y_t/f_t), equation (6) may then be written in a form amenable to multiple regression[1]:

$$(8) \quad \ell n\left(\frac{U_{t+1}}{U_t}\right) = a - \frac{b}{q^{m-1}}\,U_t^{m-1} + c\,\frac{U_{t-r}}{U_t} - qf_t$$

This is among the simplest possible estimation procedures available for a model of this type. For a fixed shape parameter (m), the model is linear in the parameters and may be estimated by multiple linear regression; for variable m, non-linear procedures are required. Our experience with this model indicates that constraints on m are necessary to avoid spurious data fits and biologically unreasonable parameter estimates. We have adopted the approach of holding m constant and iteratively searching for the value of m which minimizes the residual sums of squares of the model. A subjective evaluation of parameters is also made to ensure biologically reasonable results (e.g., the signs and relative magnitude of the coefficients are examined). Pella and Tomlinson (1969) describe a more complex estimation scheme for their general production model. Fox (1975) provides an alternative estimation method predicated on the assumption that equilibrium conditions may be approximated by averaging effort over a period of years. Fletcher (1978) and Rivard and Bledsoe (1978) provide guidance on fitting a reparameterized Pella–Tomlinson model. For the estimation method employed in the present analysis, we note that the dependent variable is the difference between successive estimators of CPUE and this term will be sensitive to errors in estimation of CPUE. Parameter estimates may therefore be characterized by high standard errors (Pella and Tomlinson 1969). It should be further noted that there is a slight confounding of the independent and dependent variables in (8). Accordingly, we have made no attempt to evaluate goodness of fit based on equation (8). We assume that catch and effort are measured without error. Considerably more complex estimation procedures are necessary if this condition is not met.

Clearly, the use of a density-independent recruitment term may not be appropriate. A preferable approach would be to consider a more realistic stock-recruitment submodel such as the Ricker or Beverton–Holt models or their generalizations (Deriso 1980, 1981; Shepherd 1982; Saila and Lorda in press). Use of a more complex recruitment function necessitates a nonlinear fitting procedure and, in general, does not allow an analytical solution for maximum equilibrium yield or optimal fishing effort. If the form of recruitment model is unknown, a quadratic function may be taken as a first approximation. Jensen (1984) employed a quadratic recruitment function as an approximation to the Ricker stock recruitment model. Optimal harvesting strategies for the simple case where both the recruitment term and the natural mortality-growth component are quadratic are described in the Appendix. In the Applications section, we primarily consider the density independent form but also illustrate use of the quadratic recruitment submodel. We have not considered other recruitment functions in the context of the delay-differential model, but do illustrate use of the Ricker and Beverton–Holt models in the context of the delay-difference model.

B. DELAY-DIFFERENCE MODEL

In this section, a simplification of Deriso's (1980) age-structured model is described. Knife-edge selection is assumed in this analysis. Although Deriso's model can accommodate a partial selection pattern, subsequent analyses have indicated that the error introduced by assuming knife-edge selection may be small (Deriso 1981 and personal communication). Possible errors introduced by this approximation should, of course, be examined for each individual species or stock.

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[1] We note that in the difference equation approximation, these terms are actually replaced by their time averages. Thus fishing mortality rate (qf_t) is applied to average biomass during the year rather than to an instantaneous measure of biomass.

The simplified delay-difference model is predicated on the assumption that, for a highly exploited stock, an exponential model for individual growth in weight is adequate since relatively few individuals will be near the asymptotic size. Further, under these conditions, recruitment rather than growth would be expected to dominate production and errors introduced by the simple growth model may not be large. Jensen (1984) employed an exponential growth function in a production model with explicit growth, mortality and recruitment terms. The growth model may be written:

$$(9) \quad w_{i,t+1} = w_{i-1,t}\, exp\,(g)$$

where $w_{i,t+1}$ is the weight of an individual at age (i) and year ($t+1$) and g is the instantaneous growth coefficient. The population biomass at time $t+1$ is given by

$$(10) \quad B_{t+1} = \sum_{i=r+1}^{\infty} w_{i,t+1}N_{i,t+1} + w_{r,t+1}N_{r,t+1}$$

where r is the age at recruitment and N_i indicates population number at age (i). Substituting the growth function (9) and noting that $N_{i,t+1} = s_tN_{i-1,t}$, where s_t is the survival fraction, we have

$$(11) \quad B_{t+1} = B_ts_t\exp\,(g) + w_{r,t+1}N_{r,t+1}$$

The survival fraction may be partitioned into natural survival (assumed to be age and time invariant) and escapement from the fishery [$s_t = \exp(-M-qf_t)$; Schnute (1985)]. We can then write:

$$(12) \quad B_{t+1} = B_t\exp\,(g-M-qf_t) + G(B_{t+1-r})$$

where M *is the natural mortality rate,* q is the catchability coefficient, f is fishing effort and $G(B_{t+1-r})$ is the spawner-recruit function (described below). The catchable stock is taken to be comprised of mature individuals. If a constant unknown fraction of the exploited stock is immature, this fraction is subsumed in coefficients of the stock-recruitment relationship.

Following Schnute (1985), we note that $B_t = Y_t[1-\exp(-qf_t)]^{-1}$. We may therefore write

$$\begin{aligned}(13) \quad & Y_{t+1}[1-\exp(-qf_{t+1})]^{-1} = \\ & Y_t[\exp(g-M)](\exp(qf_t-1))^{-1} + \\ & G[Y_{t+1-r}(1-\exp(-qf_{t+1-r}))^{-1}]\end{aligned}$$

To illustrate the simplification due to the exponential growth model, we note that the equivalent expression using the Brody-von Bertalanffy growth function and assuming knife edge selection is:

$$\begin{aligned}(14) \quad & Y_{t+1}[1-\exp(-qf_{t+1})]^{-1} = \\ & (1+\varrho)[\exp(-M)]\ [\exp(qf_t)-1]^{-1}Y_t - \\ & \varrho[\exp(-2M-qf_t)]\ [\exp(qf_{t-1})-1]^{-1}Y_{t-1} + \\ & G[Y_{t+1-r}(1-\exp(-qf_{t+1-r}))^{-1}].\end{aligned}$$

where ϱ is the Ford growth coefficient. Schnute (1985) gives a more complex expression with a slightly different form of the growth model.

Ludwig and Walters (1985) indicated that it will be difficult to extract biologically meaningful parameters for the full Deriso model using catch-effort data alone and that a much simplified production model often performs as well. The model presented here is intermediate in complexity between the Deriso-Schnute model and that of Ludwig and Walters. We have deliberately used a simplified form in recognition of difficulties in parameter estimation. In addition, we have employed estimates of the catchability coefficient derived earlier in fitting the delay-difference model and have not attempted to estimate q. Note that we have assumed that spawning precedes fishing mortality.

For simplicity we have considered only the Ricker (15a) and Beverton-Holt (15b) models as recruitment functions:

$$(15a) \quad G(B_{t+1-r}) = hB_{t+1-r}\exp(-kB_{t+1-r})$$

$$(15b) \quad G(B_{t+1-r}) = h'B_{t+1-r}/(k'B_{t+1-r}{}^{-1})$$

where B is the spawning stock biomass, and h, k, h', and k' are coefficients. Deriso (1980), Shepherd (1982), Schnute (1985), and Saila and Lorda (1986) describe three alternative parameter stock recruitment functions. We have sought to retain a simple model structure and do not consider the generalized models. If the recruitment function is given by a Ricker model, the equilibrium catch is:

$$(16a) \quad Y^* = \left\{ \left[\frac{1-\exp(-qf)}{k}\right]\cdot \ell n\left[\frac{h}{1-\exp(g-M-qf)}\right] \right\}$$

For the Beverton-Holt model, the equilibrium catch is given by

$$(16b) \quad Y^* = \left\{ \left[\frac{1-\exp(-qf)}{k'}\right]\cdot\left[\frac{h'}{1-\exp(g-M-qf)}-1\right] \right\}$$

The maximum equilibrium yield and optimal fishing effort are readily determined by evaluating these functions.

APPLICATIONS

New Zealand Rock Lobster

The two delayed recruitment models were applied to an annual series of catch and effort data for the New

Zealand rock lobster, *Jasus edwardsii*, fishery for the period 1945-75 (Saila et al. 1979). The only measure of effort available for the entire period was number of vessels participating in the fishery, however, Saila et al. (1979) demonstrated that this index of effort was closely related with a more detailed measure of effort (total number of days fished) available for the period 1963-74. Annala (1983) provided additional recent catch-effort data and updated estimates of maximum equilibrium yield.

Delay terms of 4-6 yr were considered for the delay-differential model a lag of 4 yr resulted in the greatest reduction in residual sums of squares. Delays of 4-5 yr are considered appropriate for this fishery (J. Annala, personal communication). The shape parameter (m) was set at $m = 1.1$.

Parameter estimates for the delay-differential model and their standard errors are provided in Table 1. The standard error of the recruitment term was high relative to the parameter estimate. This result is not unexpected given the overly simplistic functional form of the recruitment term used in this analysis.

A plot of the equilibrium relationship between yield and fishing effort is provided in Fig. 1. The estimated level of maximum equilibrium yield (MEY) was 4400 t at an optimal effort of approximately 770 vessels. Saila et al. (1979) estimated MEY and optimal effort to be approximately 4200 t and 780 vessels respectively based on the Fox model using an equilibrium approximation. Annala (1983) subsequently estimated MEY to range from 4000-5500 t at effort levels of 700-1000 vessels based on additional data and depending on various assumptions regarding the period of averaging.

Parameters of the delay-difference model for the New Zealand rock lobster fishery were fit by non-linear least squares (Table 2). Use of the Ricker model as the recruitment function resulted in a significantly better fit to the data and the Beverton-Holt model was not considered further. A time delay of 5 yr was found to result in the greatest reduction in residual sums of squares. Maximum equilibrium yield for the delay-difference model was 4500 t at an optimal level of effort of 730 vessels (Fig. 1, Table 2). The delay-difference model therefore indicates a slightly higher MEY at a lower level of optimum effort than the delay-differential production model. We note, however, that the curve is mildly convex and that little differentiation in yield is evident at intermediate levels of effort. Performance of the two models is consistent, despite distinct differences in model structure. Both models indicate a decline in yield at higher levels of effort. Annala (1983) reported that landings did in fact decrease further with increases in effort. Effort levels during 1976-79 averaged 1711 vessels while yield decreased to 3530 t (Annala 1983).

Trends in observed and fitted biomass indices (catch-per-unit-mortality; see Schnute 1985) are provided in Fig. 2. It is clear that the autoregressive structure of the delay-difference model dominates its predictive capability. Indeed, little biological interpretation can be put on the estimate of the growth-natural survival term since this parameter clearly plays the role of a first-order autoregressive coefficient.

American Lobster

Annual yield and fishing effort, measured as number of traps fished, was available for the USA American lobster fishery for the period 1942-78 (New England Fishery Mangement Council 1983). It was recognized that the index of effort was useful only as a rough approximation to effective effort. A more detailed measure of effort (number of trap-haul-set-over-days) available for the dominant lobster producing state (Maine) for the period 1968-78 (Thomas et al. 1983) was not highly correlated with the number of traps fished (Spearman's rank order correlation coefficient;

TABLE 1. Parameter estimates and standard errors for the generalized production model with a discrete lag. The general production model with density independent recruitment was fit for the New Zealand rock lobster and the American lobster fisheries (Eq. 8). A quadratic recruitment function was used for the Western rock lobster fishery. Absolute values of the parameter estimates are given.

	New Zealand rock lobster		American lobster		Western rock lobster	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
a	6.312	3.229	6.170	3.323	0.328	0.657
$^*b_o$	4.848	2.409	8.563	4.737	0.142	0.200
c	0.034	0.152	0.030	0.115	0.279	0.509
$^{**}d_o$	—	—	—	—	0.079	0.139
q	0.746×10^{-3}	0.322×10^{-3}	0.468×10^{-6}	0.223×10^{-6}	0.052×10^{-6}	0.044×10^{-6}
m	1.1	—	0.9	—	2.0	—
Lag	4 yr		5 yr		3 yr	
MEY	4.4×10^3 t		14.2×10^3 t		8.0×10^3 t	
F_{opt}	780 vessels		1.5×10^6 traps		5.8×10^6 std. units	

$^*b_o = b/q^{m-1}$ (See Eq. 8).
$^{**}d_o = d/q$ (See Eq. A3).

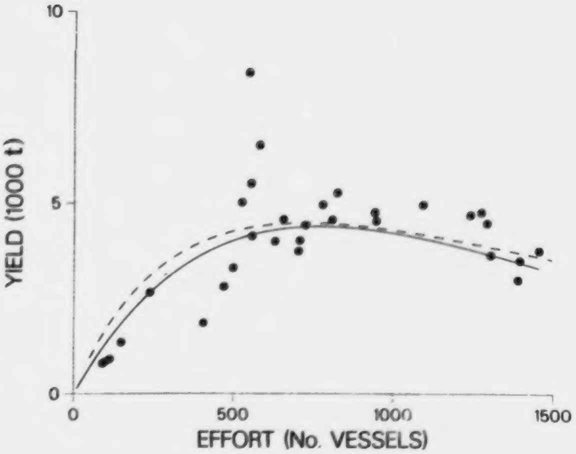

FIG. 1. Equilibrium yield-effort curves using the delay-differential (solid line) and delay-difference (dash-line) models for the New Zealand rock lobster fishery (1945–75). Solid circles indicate the observed catch and effort data.

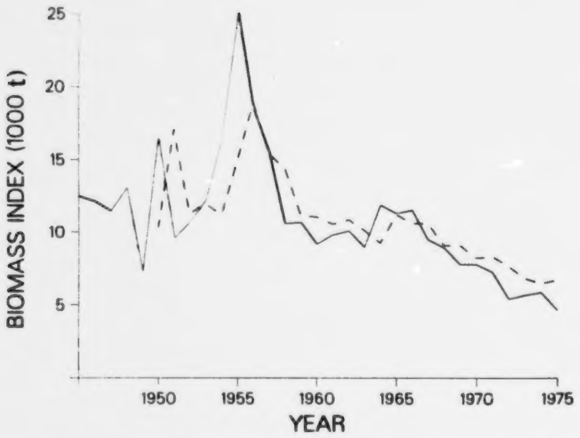

FIG. 2. Observed (solid line) and fitted (dash-line) biomass indices (catch-per-unit-mortality) for the New Zealand rock lobster fishery (1945–75), using the delay-difference model.

$r = 0.56$, $P < 0.10$). Therefore, management implications of any analysis based on number of traps, without further adjustment should be viewed with caution. A delay of 5–7 yr between spawning and recruitment is considered typical for this species (Wilder 1953). Hughes and Matheissen (1962) described growth of laboratory-reared individuals; most attained legal size by age 5. With a lag of 5 yr, the estimated MEY was 14 200 t at an optimal applied effort level of 1.46 million traps. Parameter estimates are provided in Table 1 and the equilibrium relationship between yield and fishing effort is depicted in Fig. 3. A previous estimate of MEY for the USA American lobster fishery of 14 800 t (f_{opt} = 1.59 million traps) was made in support of a coastwide lobster management plan (New England Fishery Management Council 1983) based on the Pella–Tomlinson model.

Parameter estimates for the delay-difference model are provided in Table 2. The best fit was attained with use of the Beverton–Holt model as the recruitment function with a time delay of 5 yr. In contrast to the delay-differential model, the delay-difference model was nearly asymptotic within the range of observed fishing effort levels (Fig. 3). The maximum equilibrium yield was 13 500 t. We suggest that an arbitrary but relevant target level of fishing effort for flat-topped peak production curves is the point at which 95% of the yield is attained. For the American lobster fishery, this level occurs at approximately 1.2 million traps. Although this target level is below the optimum effort indicated for the delay-differential model, we note that the equilibrium curve is mildly convex and that there is little change in yield in the range 1.0–1.5 million traps. A direct comparison of the two models is difficult due to differences in model structure and fitting procedures. The delay-differential model appeared to provide a somewhat closer fit to much of the transitional catch and effort data. We note, however, that there need not be a close correspondence between the transitional (non- equilibrium) data and the equilibrium curve. It is interesting to note that decline in yield predicted by the delay-differential model at higher effort levels has not occurred. In fact, yields increased to an average of 18 000 t during 1980–83 (Fogarty and Idoine 1985) with

TABLE 2. Parameter estimates for the simplified delay-difference model. Separation of natural survival and growth components is not possible with this parameterization of the model. The catchability coefficient was set to the value obtained in the delay-differential model.

Parameter	New Zealand rock lobster	American lobster	Western rock lobster
$\exp(g-M)$	0.809	0.855	0.542
$h^{(')}$	1.003	4.152	0.9076
$K^{(')}$	0.059×10^{-3}	0.239×10^{-3}	0.013×10^{-6}
LAG	5 yr	5 yr	3 yr
MEY	4.5×10^3t	13.5×10^3mt	8.8×10^3t
f_{opt}	730 Vessels	1.2×10^6 traps*	6.3×10^6 Std. units*

*Effort at which 95% of MEY is attained.

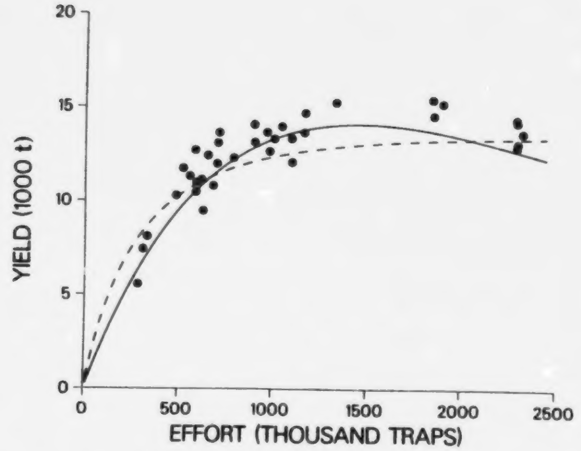

FIG. 3. Equilibrium yield-effort curves using the delay-differential (solid line) and delay-difference (dash-line) models for the American lobster fishery (1942–78). Solid circles indicate the observed catch and effort data.

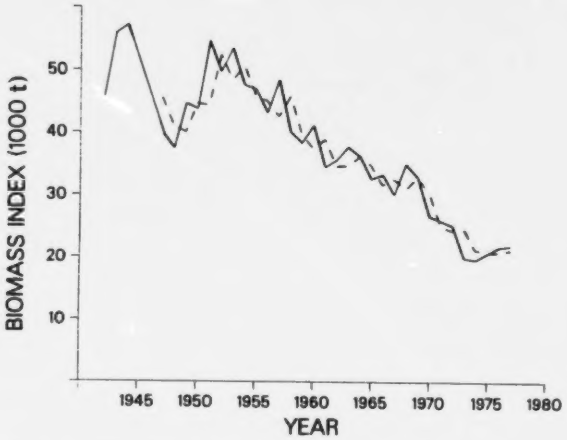

FIG. 4. Observed (solid line) and fitted (dash-line) biomass indices (catch-per-unit-mortality) for the American lobster fishery (1942–78) using the delay difference model.

a continual escalation of fishing effort. In contrast, the delay-difference model does not predict a decrease in yield at these higher effort levels although catches during 1980–83 still exceeded the predicted yield.

Trends in biomass indices (catch-per-unit-mortality) predicted by the delay-difference model are provided in Fig. 4.

Western Australian Spiny Lobster

Morgan (1979) made a detailed analysis of several alternative surplus production models, including the delayed recruitment model of Marchesseault et al. (1976), for the Western Australian spiny lobster fishery during the 1944–45 to 1976–77 fishing seasons. Fishing effort was carefully standardized for seasonal changes in catchability prior to analysis (Morgan 1979).

Attempts to fit the generalized delay-differential model for lags of 3–5 yr and alternative values of (m) resulted in parameter estimates which were not biologically reasonable except for a lag of 3 yr and $m=2$, corresponding to the delay model previously fit by Morgan (1979). The maximum equilibrium yield as determined by Morgan (1979) based on the Marchesseault et al. (1976) delayed recruitment model was approximately 8000 t. The corresponding optimal effort level was 5.8 million standard units (Morgan 1979). Since Morgan (1979) previously provided estimates for the case where $m=2$ and $r=3$ yr, we have taken this opportunity to illustrate the use of the quadratic recruitment model (see Appendix). Parameter estimates are provided in Table 1 and the equilibrium yield-effort relationship is depicted in Fig. 5. One consequence of use of a more complex recruitment function was a decrease in precision of the parameter estimates, due primarily to relatively high correlations among some parameters. Nevertheless, the estimated MEY level of 7980 t and f_{opt} of 5.8 million standard units agreed well with estimates provided by Morgan (1979) which ranged from 7965 to 8557 t at 5.6–5.9 million standard units.

The best fit for the delay-difference model was attained with a Ricker recruitment function. The equilibrium curve for the delay-difference model was nearly asymptotic (Fig. 5), in contrast to the convex form of the delay-differential model with a quadratic recruitment function. Maximum equilibrium yield was 8800 t; 95% of the MEY level was attained at approximately 6.3 million standard units. A comparison of the delay-differential and delay-difference models is again instructive. The delay-differential model appeared to conform more closely to the transitional catch and effort data at intermediate effort levels. However, the predicted decline in yield with further increases in effort has not occurred. Yield for the 1982–83 season was 12 400 t, while effort has continued to increase (B. Phillips, CSIRO, Marine Laboratory, P.O. Box 20, North Beach, W. Australia, 6020, personal communication).

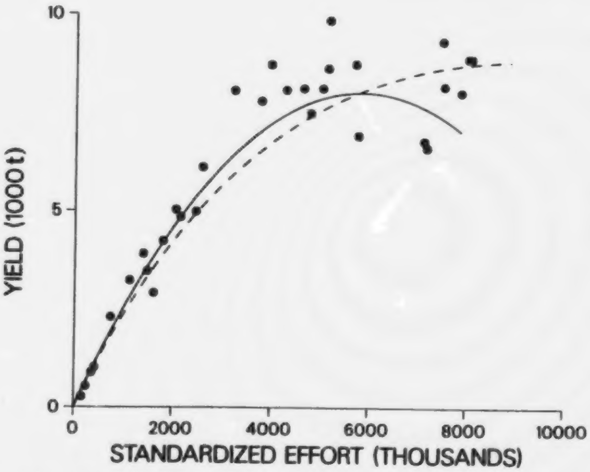

FIG. 5. Equilibrium yield-effort curves using the delay-differential (solid line) and delay-difference (dash-line) models for the western rock lobster fishery (1944/45–76/77 seasons). Solid circles indicate observed catch and effort data.

Morgan (1979) also noted that there was, in fact, little indication of a decrease in yield at higher levels of effort in this fishery.

A plot of catch per unit mortality is provided in Fig. 6. It is again clear that the autoregressive structure of the model dominates its predictive capability.

Dynamic Pool Models

Considerable recent research in invertebrate population dynamics has been aimed at developing more realistic forms for the second major class of assessment methodologies: dynamic pool yield models. Central to the Beverton–Holt, Ricker, and Thompson–Bell type calculations are that: (a) growth and natural mortality rates are unrelated to stock density, (b) recruitment is constant, (c) fishing mortality is distributed over the entire exploitable stock, and (d) population dynamic processes can be integrated over a series of annual cycles to provide a cumulative evaluation of the yield potential of population cohorts. These assumptions are clearly deficient for a variety of invertebrate stocks. More realistic models specific for sedentary populations have focused on the fact that shellfish stocks may be spatially segregated into discrete subcomponents and managed accordingly (Caddy 1975; Allen 1979; Sluczanowski 1984; Mohn and Robert 1984). Within each of these areal subcomponents there may be density dependent effects on growth, natural mortality, and subsequent recruitment. Because of the discontinuous growth of crustaceans, assumptions of annual integration of mortality and growth rates for evaluating cohort yields may be invalid. Accounting for the probabilistic annual molting frequency in the growth function for crustacea is a major requisite for more realistic yield models for this group.

In this section we outline additional approaches to yield-per-recruit analyses for invertebrate populations with consideration of factors such as density-related and environmental effects on growth, seasonal mortality rates, and discontinuous growth of crustacea. We first describe a model which allows density dependent growth and differential harvesting patterns for sedentary mollusc populations. Density-dependent growth of bivalves has been inferred for several exploited mollusc stocks including the sea scallop (*Placopecten magellanicus*) in the Georges Bank region (Caddy 1975) and the cockle (*Cardium edule*) in South Wales, U.K. (Hancock 1973). The model allows manipulation of stock density within selected subareas occupied by the stock. Total yield of the stock (summation over all areas) may thus be simulated as a combined function of different harvest scenarios for each location.

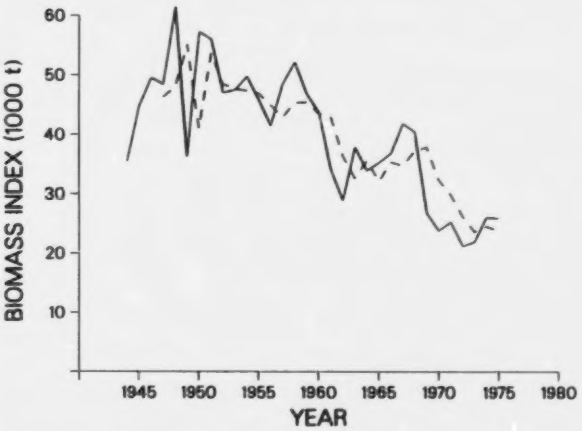

FIG. 6. Observed (solid line) and fitted (dash-line) biomass indices (catch-per-unit-mortality) for the western rock lobster fishery (1944/45–76/77 seasons) using the delay-difference model.

We next describe yield analyses for crustacean populations in which the growth component is separated into molt increment (size increase on molting) and intermolt duration. Methods of incorporating environmental or density-related effects on growth are discussed and effects of seasonal growth and mortality rates are included in a yield analysis for the American lobster.

The basic form of the proposed yield-per-recruit model for sedentary molluscs is that of Thompson and Bell (1934):

$$(17) \quad Y = \sum_j \sum_i \left\{ \frac{F_{ij}}{Z_{ij}} [1 - \exp(-Z_{ij})] \bar{w}_{ij} N_{ij} \right\}$$

where: Y = yield in weight over the life span of a cohort, F_{ij} is the instantaneous fishing mortality rate at age i and location j, Z_{ij} represents total instantaneous mortality ($Z_{ij} = F_{ij} + M_{ij}$ and M_{ij} is instantaneous natural mortality rate at age), $\bar{w}_{ij}$ is the mean weight in the catch and N_{ij} is the number of a cohort at age i and location j. The age-specific fishing mortality term may be separated into a nominal fishing mortality component (F_{nom}) and a partial recruitment multiplier (PR_i).

The spatial segregation of a stock may be represented by a two-dimensional matrix (nxm) of grid locations. Total yield from the stock is then a summation of individual yields from each grid location (j) and time period (t). Different harvesting strategies within each block may be simulated by a second fishing mortality rate multiplier (FMUL) that is location-specific:

$$(18) \quad F_{ij} = F_{\text{nom}} * PR_i * \text{FMUL}_j$$

and where PR_i is a partial recruitment multiplier allowing for differential fishery selectivity by age. Total cohort yield is then a function of location and age-specific fishing mortality rates, initial number of animals in each block (density), and natural mortality rates and mean catch weights at age in each block. Different starting densities of animals can be assigned for each block. Overall yield-per-recruit is computed by dividing the summation of yields from all blocks, by initial numbers in all locations.

Relationships between stock density and $\bar{w}_i$ may be given as linear or nonlinear age-specific functions. For example:

$$(19) \quad \bar{w}_i = u_i - v_i \log N_i$$

where u_i and v_i are linear model parameters for slope and intercept of the relation of mean weight at age on stock density (in numbers of animals). Equations are then solved at the beginning of each time period for each grid block to derive the appropriate mean weight values at age. Similar relationships between density and natural mortality could be accommodated if sufficient data were available.

Different considerations were necessary for developing yield-per-recruit models for crustacean stocks. Crustacean growth may be separated into two components, molt frequency and molt increment. The former appears to be more sensitive to environmental effects. For example, Ennis (1981) demonstrated a direct relationship between molting probability and cumulative temperature for the American lobster. Molt probability may be modeled as a function of size and temperature as:

$$(20) \quad p_{c\ell} = \frac{\exp\,(m - sCL + rT)}{1 + \exp(m - sCL + rT)}$$

where p_{C1} is the annual probability of molting by size, m, s, and r are model parameters, CL is carapace length (or some other function of size) and T is the temperature variable. Logistic models of this form have been previously used to describe molt probabilities for the King crab, (*Paralithodes camtschatica*), (McCaughran and Powell 1977) and the American lobster (Fogarty et al. 1982) although only size-related effects were considered. Additional variables could be included if sufficient information was available.

Annual growth is typically expressed as the product of molt probability and molt increment. Molt increment is generally a linear function of carapace length for exploitable-sized lobsters. The growth function in terms of weight is:

$$(21) \quad w_{c\ell,t} = a'|CL_{t-1} + p_{c\ell}(c' + d'CL_{t-1})|^{b'}$$

where the primes (′) differentiate these parameters from previously used symbols, c' and d' are coefficients of the premolt size-molt increment relationship and a' and b' are length–weight parameters. Since age determination is generally not possible for crustaceans it may be necessary to integrate over size and time:

$$(22) \quad Y = \sum_{c\ell} \sum_{t} \frac{F_{c\ell}}{Z_{c\ell}} (1 - \exp\,(-Z_{c\ell}\Delta t))w_{c\ell,t}N_{c\ell,t}$$

where all variables are defined as before. Seasonal variation in growth and mortality may be simulated by varying time scales employed in this analysis. An alternative approach which has been applied to populations of the edible crab, *Cancer pagurus* (Bennet 1979), the New Zealand rock lobster (Saila et al. 1979) and the American lobster (Caddy 1977; Fogarty et al. 1982) is to equate size classes with age groups and employ this Thompson–Bell–Ricker approach. Models of the general form of equation (22) have been constructed for the Norway lobster, *Nephrops norvegicus* (Conan and Morizur 1979) and the American lobster (Ennis and Akenhead 1978; Fogarty and Idoine 1986). Fogarty and Idoine (1986) describe a yield model with a stochastic growth component for American lobster populations. An essential feature of the framework provided by the Thompson–Bell–Ricker model is its flexibility and ability to accommodate complex growth and mortality patterns.

APPLICATIONS

Surf Clam

Density-dependent growth can be inferred for the 1976 year-class of the Atlantic surf clam, *Spisula solidissima*, off the coast of New Jersey, USA (Murawski and Serchuk 1984; H. Haskin, Rutgers University, pers. comm., Fig. 7). Growth rate of this cohort has been followed in annual surveys of the resource from 1978–84 (Murawski and Serchuk 1984). Average shell size of the 1976 year-class was similar to long-term average growth rate for the stock during 1976–80 (Fig. 8). However, since 1980, growth rate of the cohort has diverged significantly from long-term patterns. It is reasonable to assume that competition for food and space for young clams was minimal, however competition may have increased with increased size, resulting in decreasing increased size, resulting in decreased growth.

We analyzed several potential harvesting strategies for the New Jersey surf clam resource given various assumptions of the relation between density and growth, and the compensatory response of weight at age to density changes through selective fishing of heavily populated areas.

Distribution of the 1976 year-class of surf clams off New Jersey is illustrated in Fig. 9. An arbitrary 4 × 10 grid scheme was superimposed on contours of relative density of the stock. For each grid location an average density was assigned (Table 3). Long-term growth relationships (mean shell length and meat weight at age) for the New Jersey surf clam population are given in Table 3. Based on data presented in Fig. 8 the effect of density on growth rate of ages 1–4 was assumed to be

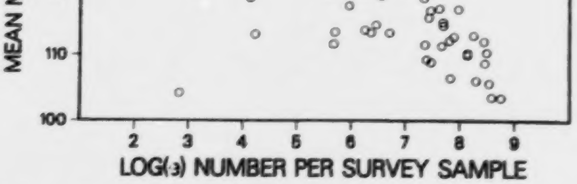

FIG. 7. Relationship between survey catch (numbers) and average meat weight (g) for surf clam, *Spisula solidissima*, off New Jersey USA. Data are for a discrete set of the 1976 year-class sampled during summer 1981. The linear regression equation is $y = 145 - 9.30(X)$.

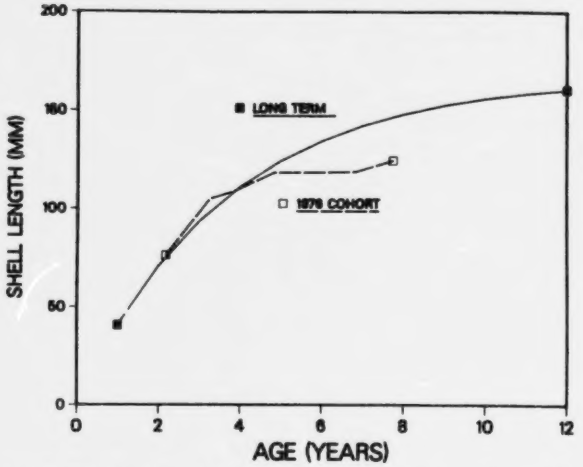

FIG. 8. Comparisons between long-term growth patterns for surf clam off New Jersey, USA, and mean shell length (mm), in annual survey samples of the 1976 year-class off New Jersey.

negligible. For all subsequent ages a linear function between stock numbers and mean weight at age was assumed (Fig. 7, Table 3). Regressions of mean weight on stock density could not be performed for each age class separately due to the lack of sufficient data. Thus, we assumed that the slope of the relationship for each age was equal to that for age 5, and changed the intercept parameter for each of the ages in the population. No data for the relation between stock density and natural mortality rate was available for this stock, thus we assumed a constant value of 0.2 for all computations. Age 5 was assumed to be the age at first selection by the fishery for intial model runs. Age at selection was changed in some additional model trials.

Five different trials were performed to compare effects of density-dependent growth on conclusions from standard yield-per-recruit analysis, and to analyze various alternative harvesting strategies for the stock (Table 4). (1) The initial run was the standard yield-per-recruit analysis assuming that growth was density independent, and no differential harvesting pattern occurred in each of the grid blocks. (2) The second run assumed mean weight-density relationships for each age class given in Table 3, but no differential harvest pattern by grid block. Additional model trials analyzed: (3) differential harvests within grid blocks depending on density, (4) effects of reducing the age at first selection, and (5) the combined effects of differential harvesting by density and a reduction in the age at first selection.

Results of model runs 1–5 are compared in Fig. 10 and 11, and Table 4. Analyses 3 through 5 assumed density-dependent growth relationships and several different potential strategies to ameliorate the negative effects of density-dependent growth on overall stock yields. Runs 3 and 5 assumed a harvest pattern where fishing mortality rate multipliers for each grid block were proportional to initial stock density in each. An arbitrary relationship of: FMUL = 0.0033 INITIAL DENSITY was assumed.

Results of runs 1 and 2 indicate a substantial negative effect of density-dependent growth rate on yield potential from the surf clam stock. Differences in yield-per-recruit assuming the two growth relationships were about 20% at low fishing mortality rates, the effect

TABLE 3. Surf clam population dynamic parameters used in simulation runs with the spatial yield model.

	Age														
Parameter	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mean Shell* Length (mm)	41	71	94	111	124	134	142	148	153	156	158	160	162	163	164
Mean Meat* Weight (g)	4	17	37	61	83	104	121	136	148	157	165	171	175	179	181
Natural Mortality Rate (*M*)	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
u value**	4	17	37	61	145	155	160	165	167	170	172	174	176	180	181
v value**	0	0	0	0	−9.30	−9.30	−9.30	−9.30	−9.30	−9.30	−9.30	−9.30	−9.30	−9.30	−9.30

Assumed Average Density (Clams/m ^{2})***

	Column									
Row	1	2	3	4	5	6	7	8	9	10
1	1	0	0	0	0	0	0	10	2	0
2	12	18	25	20	10	13	16	9	4	0
3	17	15	15	12	9	25	30	15	0	0
4	7	12	8	6	9	10	8	6	4	0

*Long-term growth relationships for surf clams in the New Jersey area.

**Assumed intercept and slope values for mean weight vs. relative density regressions. Relative densities are numbers per survey dredge tow.

***Assumed average clam densities (numbers per square meter) in a 4 × 10 spatial matrix corresponding to area occupied by the 1976 surf clam year-class off New Jersey (Fig. 5). Densities were derived by dividing average catch (numbers) of clams in survey tows by the area covered in the average tow (278 m^{2}).

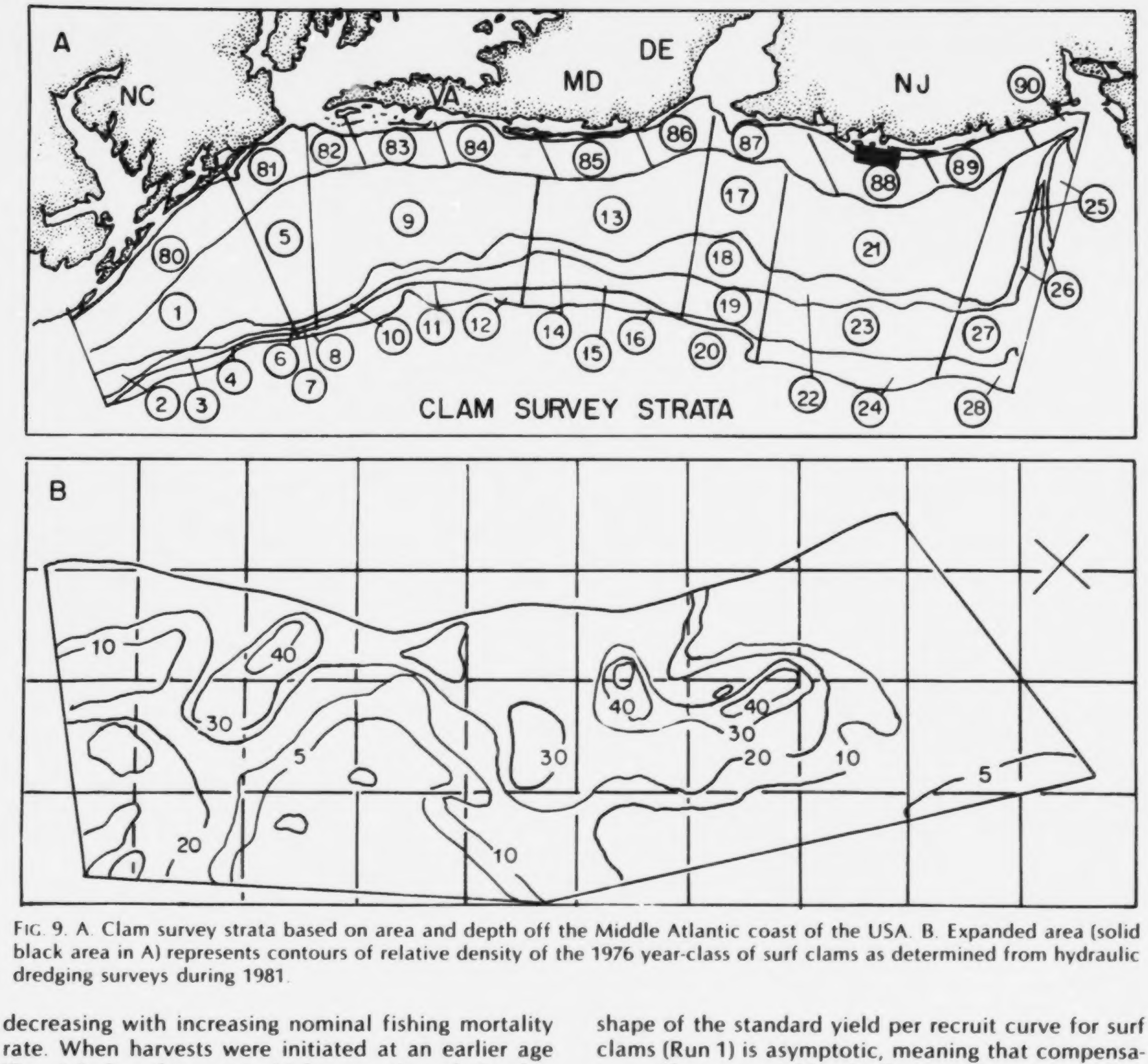

FIG. 9. A. Clam survey strata based on area and depth off the Middle Atlantic coast of the USA. B. Expanded area (solid black area in A) represents contours of relative density of the 1976 year-class of surf clams as determined from hydraulic dredging surveys during 1981.

decreasing with increasing nominal fishing mortality rate. When harvests were initiated at an earlier age (Run 4, before the age at which a negative relationship between mean weight and density was apparent) yields were nearly equal to the standard growth case for the same nominal fishing mortality rate. Although differences in yield per recruit vs. *nominal* fishing mortality rate were small between runs 1 and 4, because of the earlier age at recruitment in run 4, the cumulative exploitation rate on the stock was substantially higher, resulting in very different shapes to the plots of yield per recruit vs. exploitation rate.

Strategies employing fishing mortality rates proportional to density (Runs 3 and 5) did not result in higher yields per recruit than Runs 2 and 4. There are two potential reasons for the lack of compensatory response in yields to differential cropping of high density areas. Structure of the spatial model (equations 17–20) applied the same differential fishing mortality rate multipliers to each grid block throughout the fishable life-span, even as densities in blocks having high fishing rates were reduced to very low levels (i.e., no reallocation of fishing strategies from one year to the next). Secondly, the shape of the standard yield per recruit curve for surf clams (Run 1) is asymptotic, meaning that compensatory effects on yields of allowing clams to reach a higher proportion of their growth potential are less than for populations exhibiting a steeply descending right limb to the yield-per-recruit curve.

American lobster

Fogarty et al. (1982) described a yield analysis for offshore American lobster populations in which an empirical growth model comprised of molt increment and molt probability was employed. Growth rates were estimated based on tagging experiments conducted on the outer continental shelf of the Northeastern United States during 1968–71 (Cooper and Uzmann 1971; Uzmann et al. 1977). Probability of annual molting was estimated using a modification of the "anniversary method" (Hancock and Edwards 1967). The proportion of lobsters having molted following the first full molting period after release and prior to the succeeding molting period was determined for each group. The molting period was assumed to extend from June 1 to

TABLE 4. Calculated exploitation rates (*E*), and yields per recruit (*Y/R*, grams) for five different fishing strategies employed for surf clams.

Nominal fishing Mortality rate	Model Run 1[a]		2[b]		3[c]		4[d]		5[e]	
	E	*Y/R*	*E*	*Y/R*	*E*	*Y/R*	*E*	*Y/R*	*E*	*Y/R*
0.1	0.14	17.3	0.14	13.8	0.09	8.1	0.18	15.5	0.13	9.9
0.2	0.22	25.2	0.22	20.9	0.14	13.4	0.27	22.9	0.22	15.8
0.3	0.27	29.0	0.27	24.7	0.18	17.2	0.33	26.8	0.28	19.6
0.4	0.30	31.1	0.30	27.0	0.22	19.9	0.37	28.9	0.32	22.0
0.5	0.32	32.3	0.32	28.5	0.24	21.9	0.39	30.2	0.36	23.7
0.6	0.34	33.0	0.34	29.5	0.26	23.5	0.41	31.1	0.39	24.9
0.7	0.35	33.5	0.35	30.2	0.28	24.8	0.43	31.6	0.41	25.6
0.8	0.36	33.8	0.36	30.8	0.29	25.8	0.44	32.0	0.43	26.2
0.9	0.37	34.0	0.37	31.1	0.30	26.6	0.45	32.2	0.45	26.8
1.0	0.37	34.2	0.37	31.4	0.31	27.3	0.46	32.3	0.46	27.0
1.1	0.38	34.4	0.38	31.6	0.32	27.8	0.46	32.4	0.48	27.0
1.2	0.39	34.5	0.39	31.8	0.33	28.3	0.47	32.5	0.49	27.1
1.3	0.39	34.6	0.39	31.9	0.33	28.8	0.48	32.5	0.50	27.1
1.4	0.39	34.6	0.39	32.0	0.34	29.1	0.48	32.5	0.51	27.0
1.5	0.40	34.7	0.40	32.1	0.34	29.4	0.48	32.5	0.51	27.0
1.6	0.40	34.8	0.40	32.2	0.35	29.7	0.49	32.5	0.52	26.9
1.7	0.40	34.8	0.40	32.2	0.35	29.9	0.49	32.5	0.53	26.9
1.8	0.40	34.9	0.40	32.3	0.36	30.1	0.49	32.5	0.53	26.8
1.9	0.41	34.9	0.41	32.3	0.36	30.3	0.50	32.5	0.54	26.7
2.0	0.41	34.9	0.41	32.4	0.37	30.5	0.50	32.5	0.54	26.6

[a] RUN 1 = no density dependent growth, first selection at age 5.
[b] RUN 2 = density dependent growth, first selection at age 5.
[c] RUN 3 = density dependent growth, first selection at age 5, Fishing mortality proportional to density, FMUL = 0.0333* density (clams m^{-2})
[d] RUN 4 = density dependent growth, first selection at age 4.
[e] RUN 5 = density dependent growth, first selection at age 3, Fishing mortality is proportional to density

October 31. Skud and Perkins (1969) reported peak lobster molting activity during July-August on the outer continental shelf. Although precise molting periods are not known for offshore lobster populations, the period chosen for analysis was assumed to be representative of the primary molt season. Molt increment data were determined based on tag recoveries for all lobsters which had molted once prior to recapture. Growth curves derived for each sex are provided in Fogarty et al. (1982).

Effects of changes in fishing mortality rate and minimum legal size (MLS) limits on yield-per-recruit for male lobsters are illustrated in Fig. 12 and 13. Growth (in weight) was assumed to occur following ecdysis during

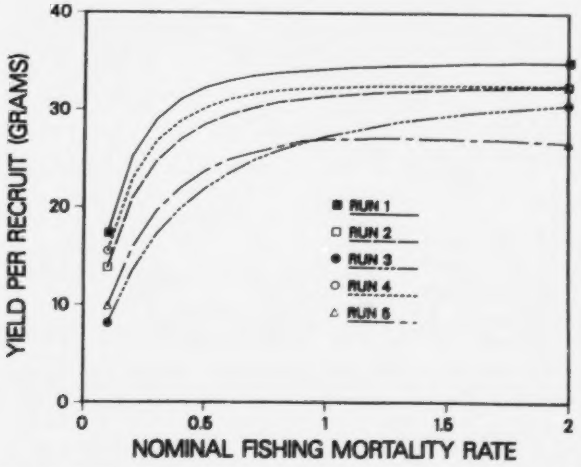

FIG. 10. Surf clam yield per recruit for five runs of the spatial yield model outlined in Table 3. Run 1 is with standard growth data and Runs 2-5 include density dependent growth rates. Harvest strategies are given in Table 4.

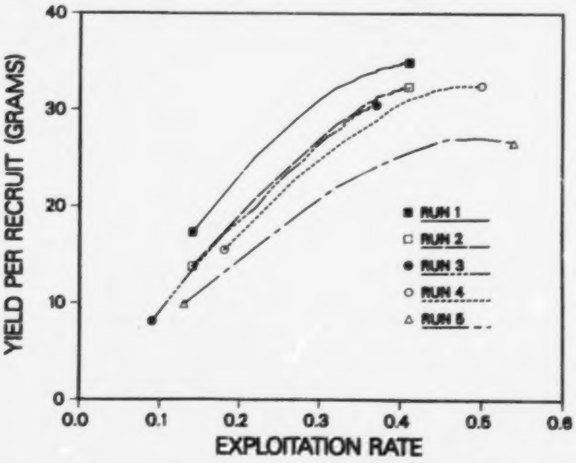

FIG. 11. Comparisons of yield per recruit for surf clams versus exploitation rate (*E*), given long-term growth patterns, and four different harvest strategies (Table 4) assuming density dependent growth.

July–September and to be complete by January when reduced metabolic activity with declining water temperature would result in a cessation in growth. Fishing mortality rates were applied on a quarterly basis and were assumed to be proportional to landings in each quarter, using 1980 as a reference year. Reduced fishing mortality rates in the first quarter (January–March) reflect lowered activity levels and catchability (McLeese and Wilder 1958) and restraints on fishing activity imposed by unfavorable weather.

Yield-per-recruit was evaluated for three levels of natural mortality ($M = 0.05, 0.10, 0.15$). Little is known concerning sources of natural mortality for lobsters. Burns et al. (1979) reviewed unpublished estimates of natural mortality and reported values of M up to 0.15. Initial analyses were performed with size at recruitment to the fishery set at 81 mm CL (current minimum legal size, or MLS). Knife-edge selection was assumed since undersized individuals may not be legally kept; survival of released sublegal sized lobsters is considered to be high.

Results are illustrated for male lobsters. Fishing mortality rates providing maximum yield-per-recruit (F_{max}) at each level of natural mortality are provided in Fig. 12. F_{max} values ranged from 0.10–0.25 under assumed natural mortality rates of 0.05–0.15. Within a broad range of fishing mortality rates, sharp reductions in F are required to effect even modest increases in yield (Fig. 12). In contrast, increases in minimum legal size limits may result in greater increases in yield (Fig. 13). Burns et al. (1979) provided yield-per-recruit estimates for offshore lobsters using the Beverton-Holt yield model; estimates of optimal fishing mortality rates were slightly higher with use of an empirical growth function in the present analysis.

Discussion

Many invertebrate stocks support valuable commercial fisheries characterized by high levels of exploitation. We have described a sequence of increasingly detailed approaches to modeling effects of harvesting on invertebrate populations. Our emphasis has primarily centered on structure of models rather than parameter estimation. Where independent estimates of growth, mortality, and recruitment are required for application of models, traditional estimation methods based on mark–recapture experiments, analysis of age or size composition, etc. may be appropriate (Ricker 1975; Gulland 1983) although special considerations may be required for application of these techniques. In many respects, difficulties in assessment of exploited invertebrate stocks parallel those in developing or artisanal fisheries and methods developed for these situations may be useful for invertebrate stock assessment (Saila and Roedel 1979; Pauley and Murphy 1982).

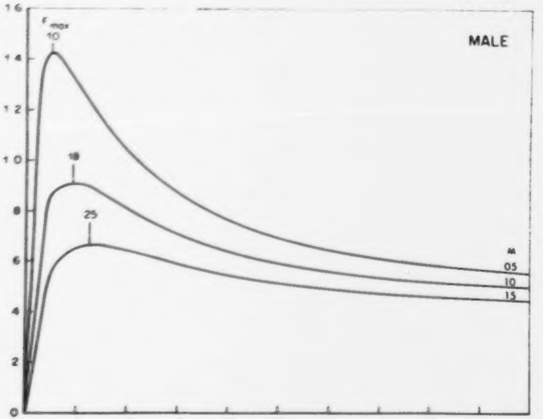

FIG. 12. Yield per recruit as a function of fishing mortality for male American lobsters by the method of Ricker (1975).

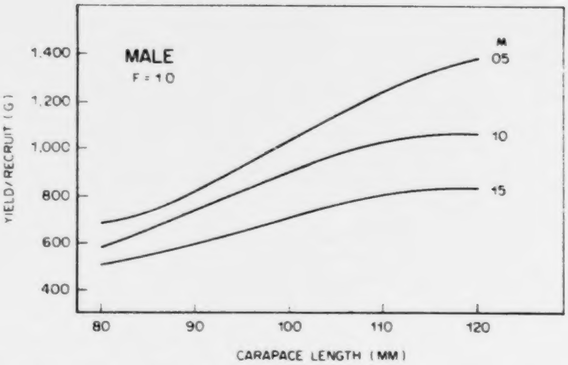

FIG. 13. Yield per recruit as a function of size at recruitment to the fishery for male American lobsters by the method of Ricker (1975).

An examination of catch and effort data from three crustacean populations indicated that delayed recruitment models provide a reasonable representation of the dynamics of these species. Estimated levels of maximum equilibrium yield and optimal fishing effort were similar for the delay models described herein and traditional surplus production models. Is there any advantage, therefore, in fitting the delayed recruitment models? We suggest that the similarity in estimated MEY and f_{opt} reflects the relative stability of populations chosen for analysis. In general, however, ignoring reproductive lags cannot yield an accurate representation of population dynamics. We also note that for species characterized by an asymptotic (or nearly asymptotic) recruitment curve, recruitment will be relatively constant over a broad range of spawning stock sizes and lagged effects will be difficult to distinguish. Nearly asymptotic recruitment curves have been demonstrated for the Western Australian rock lobster (Morgan et al. 1982) and the American lobster (Fogarty 1983; Fogarty and Idoine unpub. data).

The delay-differential and delay-difference models provided interesting contrasts in dynamic behavior for the American lobster and western rock lobster. The delay-difference model indicated a nearly asymptotic production curve while corresponding delay-differential models were dome-shaped. Recent trends in yield and effort for these species provide no evidence for a reduction in yield with increasing effort, supporting the predicted form of the delay-difference model. We note, however, that both model types assume a spatially uniform distribution of both the population and fishing intensity. Clearly, this representation is overly simplistic and it is possible that yields in these fisheries have been maintained at high levels, in part, by shifting the spatial distribution of effort.

The choice between use of the delay-differential and delay-difference models will depend on the nature of available data. If only catch-effort data are available, the fitting of the delay-differential model is simpler. It may not be possible to obtain reasonable parameter estimates for the delay-difference model based simply on catch and effort data. Even for the simplified model considered here, independent information on the catchability coefficient was required to provide an adequate model fit. Ludwig and Walters (1985) provided similar observations based on simulated data sets. If independent information for growth, mortality and/or recruitment is available, these estimates may be directly incorporated in the delay difference model. Since the model is framed in terms of biologically meaningful parameters, a more realistic representation of population dynamics should be possible. The choice of modeling approaches will therefore reflect the nature of available data with a shift toward increasingly realistic models as biological information is accrued.

We have considered only knife-edge recruitment. Partial recruitment patterns can be accommodated in both delayed recruitment models but at the expense of greater model complexity. A more detailed analysis of the species examined here would explicitly address the effect of partial recruitment. We also note that effects of measurement error in the catch and effort series on parameter estimation should be further examined. Refinement of estimates of the catchability coefficient used in fitting delay-difference models would be useful. Estimates of q for the American lobster and western rock lobster fisheries were clearly underestimates. As a result, the biomass indices (catch-per-unit-mortality) were overestimated.

The delay-difference approach accommodates seasonal patterns in reproductive activity easily while this is not strictly possible with the delay-differential model. We note, however, that in practice, a difference equation approximation is applied to the delay-differential model (and seasonality could be incorporated in the approximate form).

Considerable attention has recently been devoted to examining the predictive capabilities of models of the type considered in this paper (Stocker and Hilborn 1981; Roff 1983). We suggest an integrated approach which takes advantage of both structural models and time series analysis methodology (Box and Jenkins 1976). Although forecasts can most probably be generated more accurately using the latter approach, optimal harvesting strategies must, of necessity, be based on structural models. The delay-difference model combines an autoregressive structure with biologically meaningful parameters and thus contains elements of both approaches.

With respect to yield analyses for sedentary mollusc populations, harvest strategies considered in these examples manipulated long-term areal and age specific pattern of fishing. We did not consider a strategy wherein initial high densities of clams in some areas were cropped by differential harvest rates, then fishing mortality rates were reduced and held constant over all areas. It is likely that such a fishing strategy involving initial cropping of the stock at an early age (e.g., before the density effect on mean weights is pronounced) and subsequent reductions in age-specific F would produce yields similar to those computed for the long-term growth curve, particularly if pulse fishing of young clams is proportional to their initial density.

A critical assumption of the proposed model formulation is that if growth rate is a negative function of clam density, then strategies that reduce clam abundance from one year to the next will result in compensatory growth by the stock. The model was constructed assuming that growth compensation would be complete from one year to the next if densities were reduced. This mechanism is yet to be validated. Further, applications of the proposed model did not consider density effects on natural mortality rate. It is reasonable to assume that a positive relation between stock density and M exists since dense populations may differentially attract predators, or may result in increased stress, less food per individual, etc. for close neighbors. If both density-dependent growth *and* natural mortality rates were acting simultaneously then yields from harvest strategies aimed at reducing inhibitory densities of animals would likely be magnified.

Although the proposed model is more realistic than standard formulations, several extensions seem obvious. Our model does not consider the inhibitory effects of density on the setting (recruitment) rate of subsequent cohorts. Several studies have emphasized such a mechanism (Hancock 1973; Caddy 1975). Also, our analysis assumes that year classes are spatially discrete and can be managed as such. Although this appears to be the case for the 1976 year-class of surf clams off New Jersey, it has not been the general case for surf clams in the past. More detailed models could obviously account for density effects on recruitment and the multiple cohort situation. Finally, an extension allowing for annual changes in the areal distribution of fishing mortality, in response to dynamic changes in the relative density of animals in various compartments would allow for initial pulse fishing to control the negative effects of density, without maintaining these high fishing mortality rates throughout the life-span of the cohort.

Relationships between meat weight at age and density were available for one year for the 1976 cohort of surf clams. This relation was extrapolated for all additional ages for the population's life span. Our extrapolations were based on assuming that a linear relation between stock density and mean weight would apply for all ages, and that the slope of the relation would not change. Intercept values were scaled to allow some growth between ages even at very high densities. There is little basis for these extrapolations except convenience. Further field and/or laboratory work is obviously required in order to construct more realistic growth-density relationships over age, and to describe the compensatory response of growth to density changes.

Inclusion of environmental or density-related effects in the empirical growth model employed for crustaceans would be beneficial although information of this type is not generally available for natural populations. Difficulties in estimating growth rates, particularly size-specific molting probabilities, remain a central problem in yield-per-recruit analyses for crustaceans. We further note that high fishing mortality rates characteristic of many crustacean fisheries suggest that yield-per-recruit studies which ignore fishing-related effects on recruitment may be misleading. Accordingly, attempts should be made to couple yield-per-recruit and stock-recruitment models as advocated by Shepherd (1982).

We have proposed conceptual extensions to various standard assessment models, such that underlying assumptions of these methods more closely approximate life history aspects exhibited by invertebrate populations. In analyzing effects of these changes in model formulation, it is noteworthy that in several instances, general conclusions from analyses are similar to those derived from the application of "standard" models. Obviously, those who would argue for parsimonious model formulation would then question the necessity of more detailed models in light of their apparent marginal utility. The agreement between conclusions from "standard" and "extended" model formulations for the particular applications we analyzed, however, cannot at this point be considered to be general because so few examples have been studied. Further, data used to implement the extended analyses were collected as input to standard model formulations. As the need for more refined and sophisticated data for modeling studies is translated into new field and laboratory investigations, there may very well be significant changes in the ultimate conclusions from these analyses.

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Appendix

The general production model with an unspecified recruitment function $G\,(B_{t-r})$ may be written:

$$\text{(A1)}\quad \frac{dB}{dt} = (aB - bB^{m}) + G\,(B_{t-r}) - qfB$$

The first term allows for density-dependent growth and natural mortality. In principle, any recruitment function could be substituted for $G\,(B_{t-r})$. For example, substituting the Ricker (1954) recruitment function and expressing (A1) in terms of catch-per-unit-effort, we have:

$$\text{(A2)}\quad \ell n\,\left(\frac{U_{t+1}}{U_t}\right) = a - \frac{b}{q^{m-1}}\,U_t^{m-1} + h\,\frac{U_{t-r}}{U_t}\exp\left(-\frac{k}{q}\,U_{t-r}\right) - qf$$

In general, it will not be possible to specify an exact expression for MEY or f_{opt}, however, numerical solutions are easily obtained and should be employed if the recruitment function is known to follow a particular recruitment model.

If the form of recruitment function is unknown, an approximate form may be given by a quadratic function. Given the uncertainty of functional form of the recruitment model and recognizing the limitations of attempting to specify the recruitment component based on CPUE data alone, the approximation may be justified. The model may be expressed:

$$\text{(A3)} \quad \frac{dB}{dt} = (aB - bB^m) + (cB_{t-r} - dB^2_{t-r}) - qfB$$

Again, analytical solutions for critical points are not generally possible except for the special case where $m = 2$. For the case where both the growth-natural mortality and the recruitment components are quadratic, the maximum biomass level at equilibrium ($B^* = B_t = B_{t-r}$) is given by

$$\text{(A4)} \quad B^* = (a + c)/2(b + d).$$

The maximum equilibrium yield is then:

$$\text{(A5)} \quad \text{MEY} = (a + c)^2/4(b + d)$$

and optimal level of fishing intensity is

$$\text{(A6)} \quad f^* = (a + c)/2q$$

Finally, the equilibrium relationship between yield and fishing effort is given by:

$$Y^* = qf\left[\frac{(a + c) - qf}{(b + d)}\right].$$

At-Sea Processing and its Implications on Optimal Yield per Recruit of Alaskan King and Tanner Crabs

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SOMERTON, D. A. 1986. At-sea processing and its implications on optimal yield per recruit of Alaskan king and tanner crabs., p. 245–251. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

Fisheries for Alaskan king and tanner crabs are regulated with minimum legal carapace widths, but in recent years, it has been difficult to enforce these size limits because an increasingly greater proportion of the catch is now being processed at sea. Since the primary product form of processing vessels is cooked and frozen leg sections, it may be possible to control the catch of undersize crabs using merus lengths of processed sections as a proxy for carapace widths. In this paper, I develop merus length and carapace width relations for male *Paralithodes platypus, Lithodes aequispina, Chionoecetes bairdi*, and *C. opilio*. For *C. bairdi*, the yield per recruit obtained with the current minimum carapace width is compared to the yield per recruit where a minimum merus length is used to detect crabs smaller than the current minimum carapace width. This comparison indicates that a minimum merus length set equal to the lower 95% probability bounds of merus length at the current minimum carapace width would effectively reduce the catch of sublegal crabs without a significant loss in yield per recruit.

On réglemente la pêche du crabe royal et du crabe des neiges de l'Alaska en imposant une largeur minimale légale de la carapace, mais, au cours des dernières années, il a été difficile de faire observer ces limites de taille du fait qu'une partie de plus en plus importante des prises sont maintenant transformées en mer. Comme les produits livrés par les navires usines sont principalement des sections de pattes cuites et congelées, il est possible de contrôler les prises de crabes de taille trop petite en utilisant la longueur du mérus des sections transformées comme mesure remplaçant la longueur de la carapace. Dans cet article, je montre les rapports qui existent entre la longueur du mérus et la largeur de la carapace pour les mâles des espèces *Paralithodes platypus, Lithodes aequispina, Chinoecetes bairdi* et *C. opilio*. En ce qui concerne *C. bairdi*, je compare le rendement par recrue obtenu en utilisant la largeur minimale courante de la carapace à celui où l'on se sert d'une longueur minimale du mérus pour discerner les crabes de taille plus petite que la largeur minimale courante de la carapace. Cette comparaison montre qu'une largeur minimale du mérus qui correspond aux limites de probabilité inférieures de 95 % de la longueur du mérus pour une largeur minimale courante de la carapace réduirait efficacement les prises de crabes de taille inférieure à la taille légale sans qu'il y ait une baisse importante du rendement par recrue.

The commercial harvest of king and tanner crabs in Alaska is restricted to males having a carapace width equal to or larger than a legal minimum size. Since crabs are kept intact until processed, compliance with minimum size limits has traditionally been verified by measuring crabs while they are being unloaded at the dock. However, two recent trends in Alaskan crab fisheries have complicated enforcement of minimum size laws. First, an increasingly greater proportion of the catch is now being processed at sea by both floating processors, which buy crabs from other vessels on the fishing grounds, and catcher-processors, which are able to process the crabs they catch. Second, the incentive to keep undersize crabs has been increased by the decline in abundance of red king crab (*Paralithodes camtschatica*), the historic mainstay of crab fishermen in Alaska. Although the magnitude of the undersize catch is not known with certainty, it is potentially large and is expected to increase.

Since the usual product form of processing vessels is cooked and frozen leg sections, much of the exoskeleton is still available for examination on land. This suggests an approach to help minimize the retention of undersize crabs. If a relationship could be established between a leg dimension and the carapace width, then a minimum leg size could be defined and used either as a new legal size limit or as a tool for detecting undersize crabs. Merus length is a good candidate for such a dimension. In this paper, I develop merus length and carapace width relationships for the four most important species presently being processed at sea: golden king crab (*Lithodes aequispina*), blue king crab (*P. platypus*), and two species of tanner crab (*Chionoecetes bairdi* and *C. opilio*) from the Eastern Bering Sea (EBS). In addition, for *C. bairdi*, I examine the probable consequences of undersize catch on yield per recruit and explore several options for utilizing merus length to control this catch.

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Materials and Methods

Merus length of the second walking leg (Fig. 1) and maximum carapace width (including any lateral spines) were measured to the nearest 1 mm on 339 male *P. platypus*, 404 male *C. bairdi*, and 930 male *C. opilio* during a 1979 National Marine Fisheries Service stock assessment survey of the EBS. In addition, 343 male *L. aequispina* were similarly measured on a 1983 survey to the EBS. Sampling locations for all species are shown in Fig. 2.

Merus length was assumed to be proportional to carapace width raised to a power. On log–log axes, this relationship is

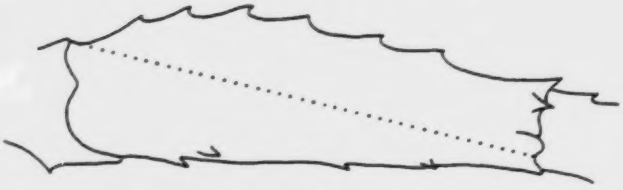
$$\log M = A + B \log C$$

where M is merus length, C is carapace width and A, B are undetermined coefficients which were estimated using linear regression. Residual plots indicated that each data set had a number of large negative deviates that probably represented measurements taken on crabs in the process of regenerating a leg. Since the number of deviant values was small, ranging from 0.5 to 1.5% of the sample, and, as discussed later, was nearly identical to the expected percent of regenerated legs for king and tanner crabs, they were deleted by sequentially removing the largest negative deviate until the tails of the residual distribution were nearly symmetric (see Somerton and MacIntosh 1983a for a more thorough discussion of this type of outlier elimination). After reestimating the regression coefficients, linear trends in residual variance were examined by regressing the squared deviations against log carapace width. Residual variance did not increase with body size (zero slope; $P > 0.05$) in any of the four cases.

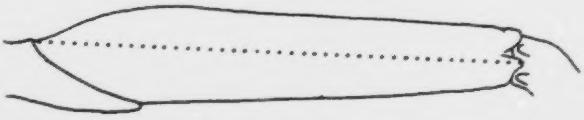
Merus length and carapace width, less outliers, were, for convenience, transformed back to a linear scale, and plotted along with the regression lines and 95% probability bonds (mean ± 1.96 standard deviations) in Fig. 3. Equations of the regression lines are shown in Table 1.

Possible Management Options

Merus length and carapace width relations can be utilized in two distinct ways to minimize the catch of undersize crabs. First, the legal minimum size laws could be redefined in terms of merus length. Second, a minimum merus length could be defined and used by officials to verify compliance with present minimum carapace width laws. Specific examples of these two options are based on the merus length and carapace width relationship for *C. bairdi*, which is shown on an enlarged scale along with the minimum legal carapace width in Fig. 4.



L. aequispina and *P. platypus*



C. bairdi and *C. opilio*

FIG. 1. Merus length definitions. Merus length of the second walking leg was measured with calipers along the dotted line shown for each species.

If the minimum size limit were to be redefined in terms of merus length, then the appropriate choice of merus length would be 124 mm (line A, Fig. 4), the mean merus length at the current minimum carapace width. Such a minimum merus length could be applied to processing vessels alone or it could be applied to all crab landings. In either case, the affected fishermen would essentially be required to measure legs in order to insure legality. Since this is more time consuming than measuring carapaces, especially for the more active species, such a redefinition of minimum size would not be welcomed by fishermen.

The second option, using the merus length and carapace width relationships to detect crabs with sublegal carapace widths, is complicated by the variability about the regression lines. For example, consider the previous situation where the minimum merus length is set equal to 124 mm, the mean at the minimum legal carapace width (line A, Fig. 4). Those crabs above horizontal line A and to the left of the vertical line have sublegal carapace widths, but would be undetectable as such because they have merus lengths greater than the 124 mm minimum. Conversely, those crabs to the right of the vertical line and below horizontal line A have legal carapace widths, but would be misclassified as sublegal because they have merus lengths smaller than the 124 mm minimum.

TABLE 1. The fitted regression equation, standard deviation of the residuals (SD), number of data after outlier deletion (n), and R square value (R^2) is shown for each species.

Species	Regression equation	SD	n	R^2
C. bairdi	$\log M = -0.238 + 1.024 \log C$	0.063	402	95.1%
C. opilio	$\log M = -0.421 + 1.079 \log C$	0.071	925	96.3%
L. æquispina	$\log M = -1.505 + 1.238 \log C$	0.052	338	93.8%
P. platypus	$\log M = -1.633 + 1.264 \log C$	0.067	334	96.5%

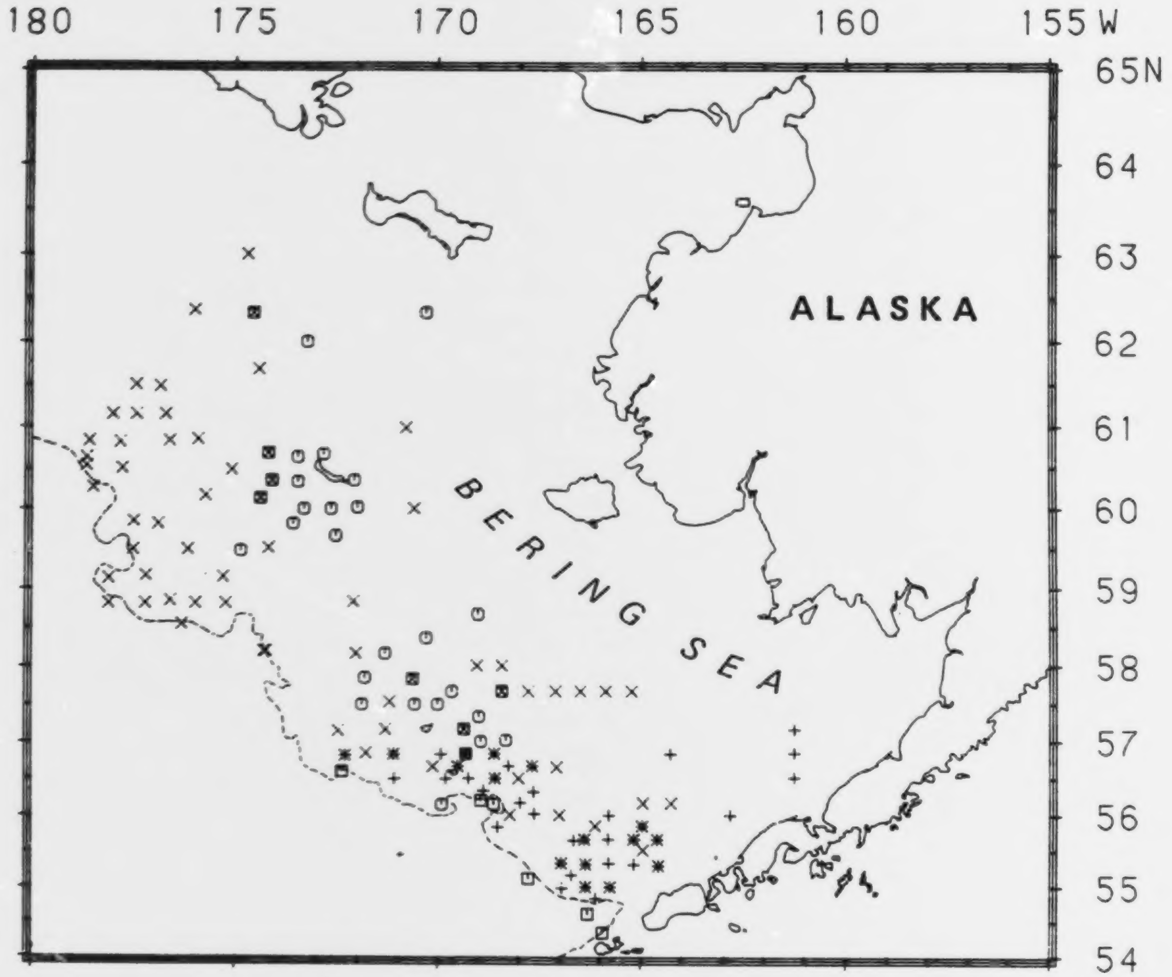


FIG. 2. Location of stations where one or more specimens of the indicated species were sampled. Species symbols are *L. aequispina* (□), *P. platypus* (○), *C. bairdi* (+), *C. opilio* (X). Stations where more than one species were sampled are shown with the species symbols superimposed. The 200 m depth contour is indicated with a dashed line.

The number of sublegal width crabs that are undetectable because they have merus lengths greater than the minimum could be reduced by increasing the minimum merus length to 141 mm (line B, Fig. 4), the upper 95% probability bound at the legal minimum carapace width. Such a change, however, also increases the number of legal width crabs that would be misclassified as sublegal because they have merus lengths smaller than the minimum. It follows that a reduction in the minimum merus length to 110 mm (line C, Fig. 4), the lower 95% probability bound, increases the nondetection rate and decreases the misclassification rate.

The ideal minimum merus size would be one that allows both a low nondetection rate of sublegal crabs and a low misclassification rate of legal crabs, but it is clear that both attributes are not obtainable simultaneously, and a choice must be made. If the catch of undersize crabs results in a decrease in the yield obtainable from the population, then it represents a loss sustained initially by honest fishermen. However, as the population decreases to its new equilibrium level, the loss will ultimately be felt by all. Increasing the minimum merus size, in an attempt to minimize this loss, would result in an increase in the number of honest fishermen who are wrongly accused of retaining undersize crabs. This method of detecting undersize crabs would lose support within the fishing community if such false accusations were sufficiently common. Considering this, I believe that a minimum merus length should be set low, for example, at the lower 95% probability bound.

If a minimum merus length were set at this size, the expected misclassification rate, or the percentage of legal size crabs that are classified as sublegal, would be calculated as follows. The misclassification rate varies with the size distribution of the catch, and reaches its maximum when the entire catch is exactly at the minimum legal carapace width (Fig. 4). Since 5% of the crabs at any specific carapace width fall outside the 95% probability bounds, it follows that, at the minimum legal carapace width, 2.5% of the crabs have meruses smaller than the lower 95% probability bound. Therefore, if the proposed minimum merus length were used to detect undersize crabs, then, at most, only 2.5%

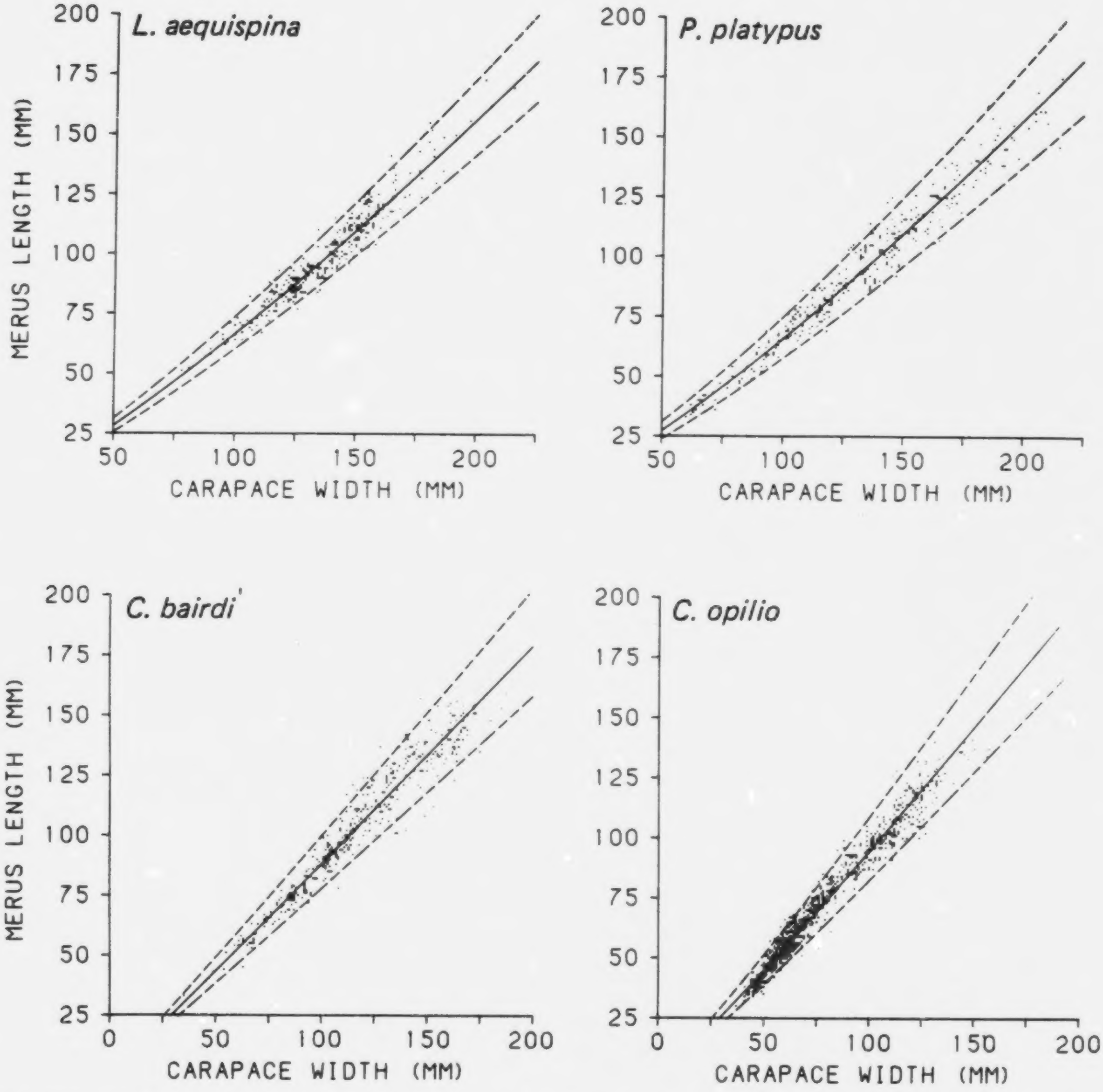


FIG. 3. Merus length and carapace width data, fitted regression line (solid line), and 95% probability bounds (dotted line) for each species. Note that the 95% probability bounds are equal to the mean ± 1.96 standard deviations, and, therefore, are not equal to the 95% confidence interval of the regression line.

of a completely legal catch would be misclassified as sublegal. In other words, a fisherman could be considered in violation of the minimum size law if more than 2.5% of a random sample of merus lengths were less than the minimum.

Such a strategy would result in a relatively high nondetection rate of sublegal crabs. For one of the four species, *C. bairdi*, the effect of this on yield per recruit will be considered in the next section.

Potential Effect of Undersize Catch on Yield per Recruit

The potential effect of undersize *C. bairdi* catch on yield per recruit (*Y/R*) was examined with a yield simulation model described in Somerton (1981a). This model assumes that: (1) carapace width increases with age according to a von Bertalanffy growth function; (2) total body weight increases proportional to carapace width raised to a power; and (3) instantaneous fishing mortality equals the 1979–83 average. Estimates of the various parameters are provided in Table 2.

The first stage of the analysis consisted of examining how *Y/R* varies with size at recruitment. Since crabs are individually measured, recruitment is knife-edge; therefore, the carapace width at recruitment equals whatever minimum size limit is in effect. Yield per recruit is shown plotted against minimum carapace size limit (Fig. 5). Note that the *Y/R* at the current 140 mm

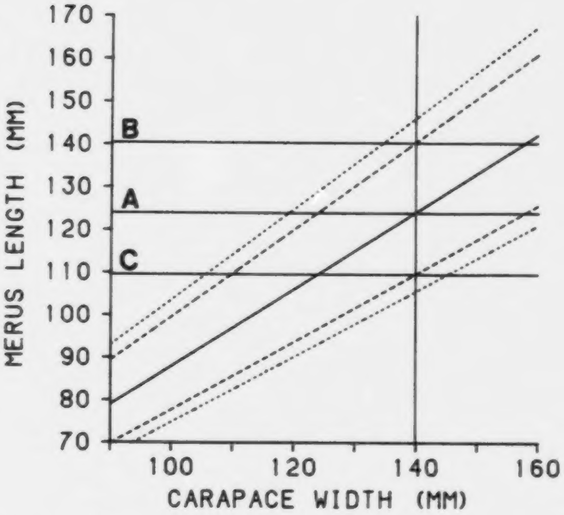


FIG. 4. Merus length and carapace width regression line (solid line), 95% probability bounds (dashed line), and 99% probability bounds (dotted line) for *C. bairdi*. The vertical line is the current minimum carapace width. The horizontal lines represent minimum merus lengths set at the probability bound (line C) of merus length at the minimum carapace width.

size limit (306.8 g) is 3.3% lower than that which would be obtained (317.4 g) if the minimum size limit were reduced to its optimum value at 127 mm. (The current *C. bairdi* minimum size limit is not optimal primarily because it was established before sufficient information for *Y/R* analysis was available.)

The current loss in *Y/R* due to the catch of undersize crabs cannot be estimated precisely because processed leg sections have not been measured. However, the worst case can be examined. In the absence of any size restrictions, a fisherman would retain crabs as small as the minimum size that can be marketed. Since *C. opilio* are apparently acceptable as small as the 98 mm minimum size limit, it is quite likely that *C. bairdi* would also be acceptable at this size. If it is assumed that all *C. bairdi* > 98 mm are retained by all fishing vessels, then the resulting *Y/R* (275.8 g) would be 10.1% less than that under the current 140 mm size limit and 13.1% less than the maximum *Y/R* that would be obtained with a 127 mm size limit. These estimates, however, are certainly exaggerated because a large proportion of the catch is landed at shorebased processing plants and is therefore subject to the 140 mm carapace width limit.

This decrease in *Y/R* is the maximum that would occur if the entire catch were processed at sea and not subject to minimum size limits. A situation is now examined in which the same fishery is subject to a minimum merus length which is used to verify compliance with a 140 mm minimum carapace width. Again, the worst case is examined, that is, it is assumed that fishermen measure legs of all sublegal crabs and retain those having merus lengths greater than the minimum.

When fishermen measure legs, recruitment is no longer knife-edge with respect to carapace width; therefore, fishing mortality is not constant, but increases to its asymptotic value over some range of carapace width. Such size-specific fishing mortality can be modeled as a product of a constant fishing mortality rate and a size-specific selectivity coefficient equal to the proportion of crabs at each carapace width that have merus lengths greater than the minimum. The proportion selected as a function of size was estimated by assuming that at each 1 mm interval of carapace width, log merus length was normally distributed with a constant standard deviation (Table 1) and a mean predicted by the merus

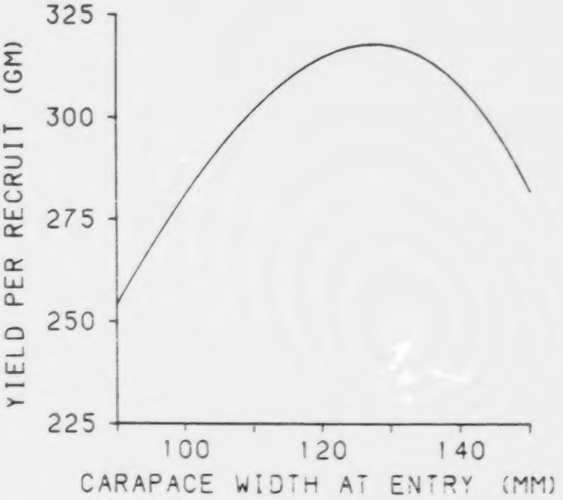


FIG. 5. Yield per recruit of *C. bairdi* as a function of minimum carapace width. Note that the yield per recruit at the current minimum carapace width (140 mm) is less than that which would be obtained at the optimum minimum carapace width (127 mm).

TABLE 2. Functions and parameter values used in the *C. bairdi* yield per recruit calculations. All values, except fishing mortality rate, were obtained from Somerton (1981a). Exploitation rate was estimated from population estimates and catch data (R. Otto, NMFS, Kodiak, AK, pers. comm.) for 1978–83. Fishing mortality rate was estimated from the natural mortality rate and the 5-year mean exploitation rate using the equation shown.

Von Bertalanffy growth equation

$$C = L_\infty (1 - e^{-k(t-t_o)})$$

C = carapace width in mm
t = age in years
L_∞ = 200
K = 0.16
t_o = 0.80

Weight-size equation

$$W = AC^B$$

W = weight in g
A = 0.00019
B = 3.10

Mortality rate

$$\mu = \frac{F}{F + M}(1 - e^{-(F + M)})$$

M = natural mortality = 0.22
F = fishing mortality = 0.79
μ = exploitation rate = 0.50

length and carapace width equation. The merus length probability distribution function at each carapace width interval was then integrated from $+\infty$ to the minimum merus size limit. The resulting estimates of proportion selected decrease from 0.967 at 139 mm to 0.005 at 106 mm (where the upper 99% probability line intersects line C, Fig. 4) to essentially zero at 98 mm. Since *Y/R* analysis requires age-specific mortality rates, proportion selected by size was transformed to proportion selected by age using the von Bertalanffy growth function for *C. bairdi* (Table 2).

The *Y/R* that would be obtained with a minimum merus length set at the lower 95% probability bound (line C, Fig. 4) is shown, along with the *Y/R* obtained with the optimum size limit, the current size limit and no size limit, in the following table.

	Y/R of (g)	% of optimum	% of current
Optimum minimum size limit (127 mm)	317.4	100.0	103.5
Current minimum size limit (140 mm)	306.8	96.6	100.0
Minimum merus length limit (110 mm)	313.1	98.6	102.1
No minimum size	275.8	86.9	89.9

Note that the *Y/R* that would be obtained with the proposed minimum merus length is only slightly less (about 1.4%) than the *Y/R* obtained with an optimum carapace width limit, but it may be considerably greater than the *Y/R* obtained with no size limit. In addition, because the current minimum size limit is not optimal, the proposed minimum merus length would provide a slight increase in *Y/R* relative to the current size limit. Considering that the *Y/R* estimates for the minimum merus limit were for an expected worst case, that is, when fishermen measure the legs of sublegal crabs, it appears that the proposed size limit would allow much of the sublegal catch to be detected with only a slight loss in *Y/R*.

A similar analysis cannot yet be done for *C. opilio, L. aequispina* or *P. platypus* because information on either growth or mortality rates is lacking. However, if the current minimum size limits maximize the yield per recruit for each species, then minimum merus lengths set at the lower 95% confidence bounds should result in yields somewhat less than the maximums but greater than those that would be obtained by unregulated fisheries.

Discussion

Valid use of the merus length and carapace width relationships to minimize the retention of sublegal size crabs is subject to three important assumptions.

First, the merus length and carapace width relationships are intended to portray the relationship between the length of a cooked and frozen merus and the carapace width of a live crab. However, since data from processed crabs were unavailable, the relationships were based solely on data obtained from live crab. If processing results in a substantial change in merus length, then the relationships are invalid for their intended use.

Second, it is implicitly assumed that the merus length and carapace width relationships are applicable over the entire geographic range of the population being managed. *Chionoecetes bairdi, C. opilio,* and possibly other Alaskan crab species, however, display considerable geographic variability in size at maturity, and presumably in growth rate, in response to variations in the temperature regime (Somerton 1981b). Although growth rate may vary, body shape should not; therefore the morphometric relationships should still be valid. However, when populations are so isolated that genetic exchange is small or nonexistent, then morphologic divergence may occur (Somerton and MacIntosh 1983b). In these cases, separate merus length and carapace width relationships must be defined for each population.

Third, the merus length and carapace width relations were based on data assumed to be free of measurements taken from partially regenerated legs; however, the inclusion of such measurements in any catch sampling program is almost unavoidable. Leg regeneration could create a problem because the misclassification rate of legal crabs will increase as the incidence of regenerated legs increases. To estimate how serious this problem might be, the expected percent misclassified due to regenerated legs was estimated for *C. bairdi* and *P. camtschatica* using data provided in Edwards (1972). The probability of not recognizing and measuring a partially regenerated leg is equal to:

$$P = P1 \cdot P2 \cdot P4$$

where

$P1$ = probability that a crab has at least one partially regenerated leg;

$P2$ = probability that the partially regenerated leg is a second walking leg;

$P3$ = probability that the section being examined has the partially regenerated leg;

$P4$ = probability that the partially regenerated leg is unrecognized.

Edwards (1972) determined that 14.7% of the adult male *P. camtschatica* and 43.0% of the adult male *C. bairdi* in the EBS have at least one leg in some stage of regeneration. On 25% of the *P. camtschatica* and 18% of the *C. bairdi* showing any leg regeneration, it was the second walking leg that was affected. Given that a crab has a partially regenerated second walking leg, the probability that it occurs in the section being examined is simply 0.50. Assuming that, on the average, six molts are required for complete regeneration (Edwards 1972) and that partially regenerated legs may be mistaken for normal legs after four molts, then the probability of not recognizing a partially regenerated leg is 2/6 = 0.33. The expected probabilities are therefore;

P. camtschatica (0.147) (0.25) (0.50) (0.33) = 0.006
C. bairdi (0.430) (0.18) (0.50) (0.33) = 0.013

Thus, approximately 0.5 to 1.5% of the crabs examined will have a partially regenerated second walking leg which will be measured and recognized as normal. Since these values are quite small, it is unlikely that leg regeneration could impair the utility of merus length as a tool for detecting sublegal crabs. In the event that geographic or temporal variation results in a pronounced increase in leg regeneration rate, additional measurements from other legs could be used to determine whether or not the second walking leg was in the process of being regenerated. This may allow rejection of partially regenerated walking legs from a sample.

From a managerial perspective, the most certain approach of minimizing the catch of undersize crabs is probably to require that fishery inspectors be aboard processing vessels; however, this may not be the most cost efficient approach, and, depending upon who was required to pay for these inspectors, it may be resisted by fishermen. The alternative approach proposed here, that is, using merus length, to verify compliance with a minimum carapace width law, would be an effective way of controlling sublegal catch without seriously reducing yield per recruit.

Acknowledgments

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EXPLOITATION AND MULTISPECIES INTERACTIONS

Population Dynamics and Fisheries of Squat Lobsters, Family Galatheidae, in Chile

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Two species of squat lobsters, *Cervimunida johni*, Porter, and *Pleuroncodes monodon*, Milne Edwards, family Galatheidae, are harvested commercially off Chile. A commercial fishery began by exploiting the first species but has gradually shifted to harvesting the second. The fishery for *Pleuroncodes* began in 1966 off San Antonio (L. 33°35"S) but has gradually moved southward and now extends to Talcahuano (37°S). There are two possible explanations for this shift in fishing area; (1) increased fishing pressure, and (2) changes in the natural environment. Some support for the second explanation is seen by simultaneous changes observed in other species which may be due to cyclic changes in the environment.

Data on the fishery has been collected from 1966 to the present from the area between Coquimbo (30°S) and Talcahuano by the Fisheries Development Institute of Chile (Instituto de Fomento Pesquero, IFOP) by monitoring the fleet at landing ports and from research surveys. From 1979 to 1983 research surveys of the fishing ground were conducted in an area from 35° to 27°S between depths of 70 to 350 m and using bottom trawls designed for catching squat lobsters.

Results of studies to date have provided information on the life history of each species, including reproductive patterns, minimum size at sexual maturity and an estimation of growth rate. Oceanographic factors hypothesized to affect *Pleuroncodes* population dynamics are discussed.

Deux espèces de galathées (*Cervimunida johni*, Porter et *Pleuroncodes monodon*, Milne Edwards, famille des galathéidés) font l'objet d'une pêche commerciale au large du Chili. Une pêche commerciale visant tout d'abord la première espèce s'est graduellement modifiée pour porter sur la seconde. La pêche des *Pleuroncodes* a débuté en 1966 au large de San Antonio (33° 35′ S de lat.) mais s'est par la suite déplacée vers le sud; elle atteint maintenant Talcahuano (37° S). Ce déplacement des aires de pêche peut s'expliquer de deux façons : 1) une augmentation de la pression de pêche et 2) une modification du milieu naturel. Des modifications observées simultanément chez d'autres espèces et pouvant être causées par des changements cycliques du milieu appuient, du moins en partie, la deuxième hypothèse.

Des données sur cette pêche sont recueillies depuis 1966 dans la région s'étendant de Coquimbo (30° S) à Talcahuano. Les données ont été obtenues par l'Institut de développement des pêches du Chili (Instituto de Fomento Pesquero, IFOP) qui effectue des contrôles de la flottille aux ports de débarquement de même que des relevés de recherche. De tels relevés des fonds de pêche ont été réalisés de 1979 à 1983 dans la région comprise entre 35° et 27° de latitude sud. Ils ont été réalisés à des profondeurs variant de 70 à 350 m à l'aide de chaluts de fond conçus pour la capture des galathées.

Les études effectuées ont permis d'obtenir des renseignements sur le cycle vital de chaque espèce, notamment sur les caractéristiques générales de la reproduction, la taille minimale à maturité sexuelle et le taux de croissance estimé. Les auteurs traitent des facteurs océanographiques que l'on suppose avoir un effet sur la dynamique de la population des *Pleuroncodes*.

Introduction

Galatheids are part of the anomura sea fauna off Chile. Five genera have been described: *Galathea* Fabricius, *Pleuroncodes* Stimpson, *Cervimunida* Benedict, *Munida* Leach, and *Munidopsis* Whiteaves. Of 16 species, 8 are endemic to Chilean waters but only two species, *C. johni* Porter and *P. monodon* H. Milne Edwards are of economic importance (Fig. 1). *Munida gregaria* Fabricius[1] and *M. subrugosa* White[1] may become economically important in the near future and *M. montemaris* Bahamonde and López may have some

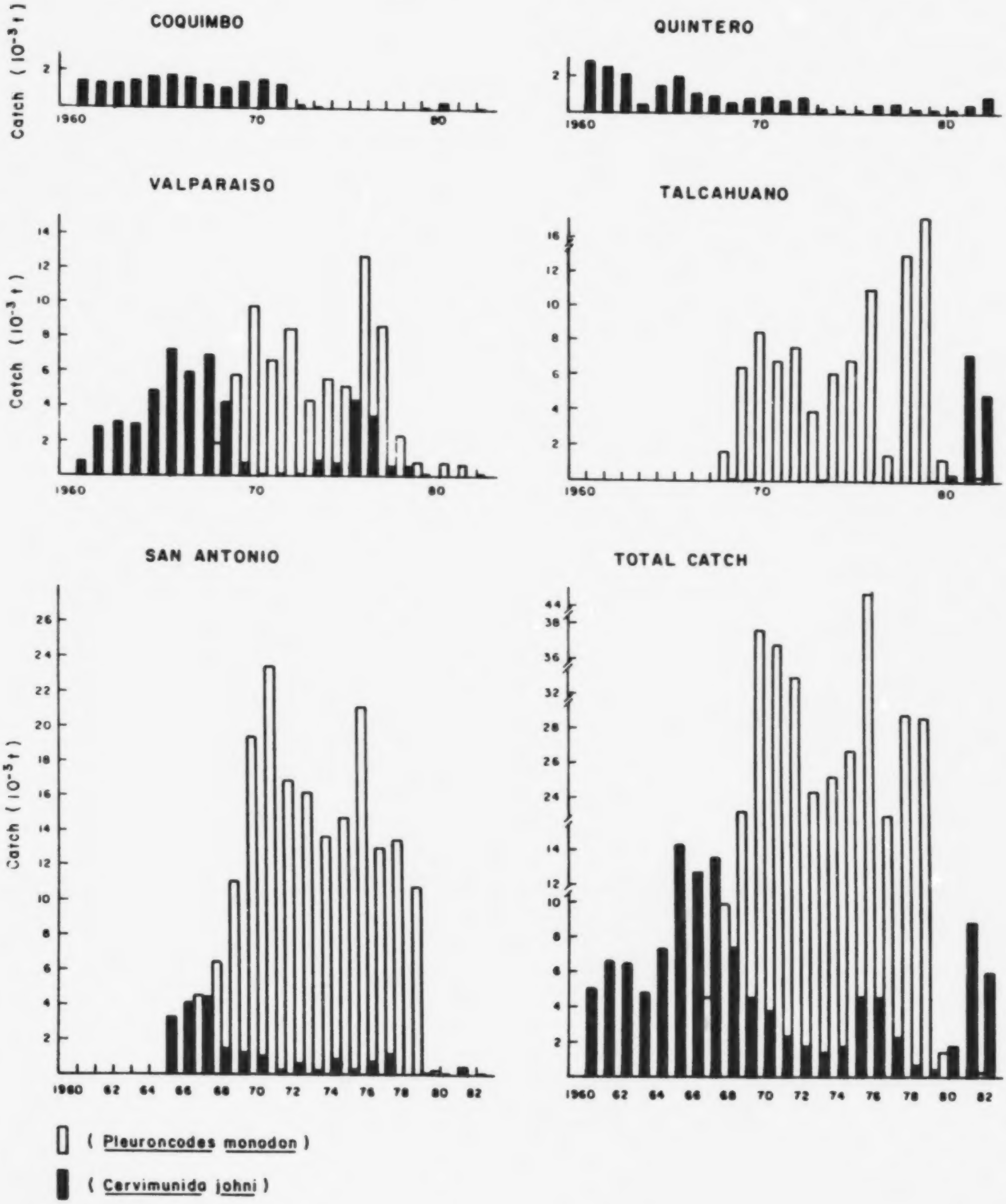

FIG. 1. Annual landings of *Pleuroncodes monodon* and *Cervimunida johni* by port and total national landings in Chile (1960–82).

importance in the distant future. The remaining species in Chilean waters are only of scientific interest.

P. monodon is distributed from Lobos de Afuera in Peru to the Bay of Ancud in Chile (Haig 1955) and occurs in depths between 20–40 m off Antofagasta (Gutierrez and Zuñiga 1977) and from 200 to 400 m off Valparaiso (Arana and Pizarro 1970) (Fig. 2). *C. johni* has a more restricted distribution and occurs between Coquimbo and Isla Mocha at depths between 200–400 m.

The Chilean squat lobster fishery began in 1953 on *C. johni* and in the last three decades, there have been numerous studies on the biology of exploited species (*C. johni*: De Buen 1957; Fagetti 1959, 1960; Alegría et al.

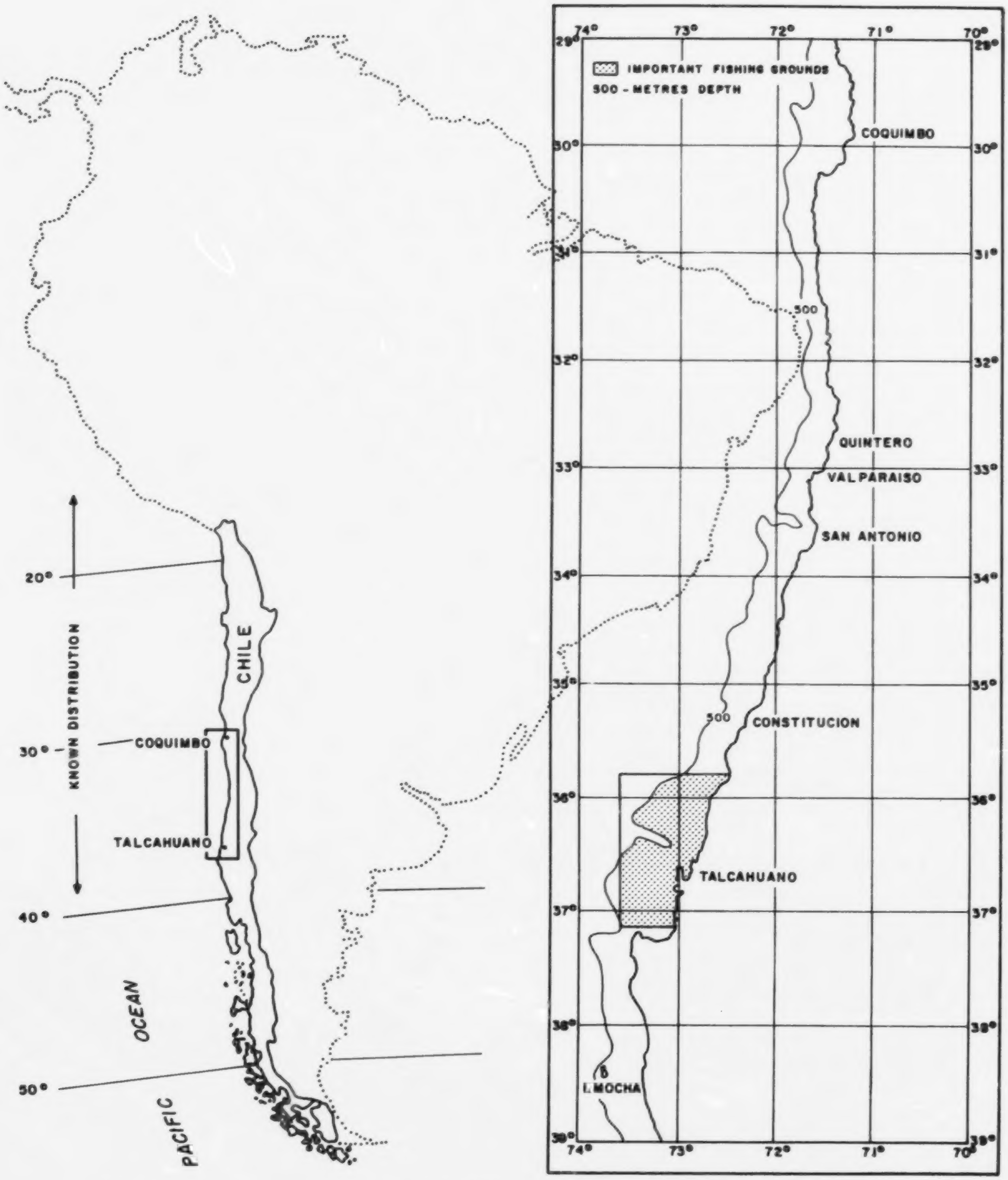
20°
KNOWN DISTRIBUTION
CHILE
30°
COQUIMBO
TALCAHUANO
40°
OCEAN
50°
PACIFIC
74°
73°
72°
71°
70°
29°
▨ IMPORTANT FISHING GROUNDS
500 - METRES DEPTH
COQUIMBO
30°
31°
500
32°
QUINTERO
33°
VALPARAISO
SAN ANTONIO
34°
35°
500
CONSTITUCION
36°
TALCAHUANO
37°
38°
I. MOCHA
39°

FIG. 2. Geographical distribution and main fishing areas for *Pleuroncodes monodon* in Chile.

1963; and Bahamonde 1965. *P. monodon*: Henríquez and Bahamonde 1964; Arana and Pizarro 1970; Fagetti and Campodónico 1971; Gutierrez and Zuñiga 1977 Henríquez 1979). In 1965 the Fisheries Development (Instituto de Fomento Pesquero, IFOP) began biological and economic studies of squat lobster fisheries to investigate additional exploitation of these resources (Mistakidis and Henríquez 1966). This resulted in a number of internal reports, mostly on *P. monodon*, many of which have not been published although the most important points have been summarized. In recent years, (G. Henríquez, unpubl. data) research has focused on why areas of highest abundance of *P. monodon* are located between 36° and 37°S (this represents a relatively small area at the southern extremity of its latitudinal range) and possible causes of the decrease in average commercial catch since 1970.

Initially in 1953 the squat lobster fishery was based entirely on landings of *C. johni* made at Coquimbo, Valparaiso and San Antonio (Fig. 2). Landings peaked at 14 365 t in 1965, and in 1966 fishing ranged from Coquimbo (19°30"S) to Punta Iloca (34°57"S) (Mistakidis and Henríquez 1966). Subsequently landings of *C. johni* declined gradually and in 1970, 3 812 t were harvested (Fig. 1). Abundance of *C. johni* gradually decreased in the area between Coquimbo and Valparaiso but catches of *P. monodon* increased as the fishing fleet moved further south. In 1967 landings of the latter species amounted to 4 583 t, increasing to 9 961 t in 1968. The best squat lobster fishing grounds were located in an area from 29° to 35°S where catches of 2 $t \cdot h^{-1}$ were made (Hancock and Henriquez 1968). In 1970, 37 678 t of *P. monodon* were caught, and fishing effort increased to 1 257×10^3 BHP (Brake Horse Power) per fishing day (Henriquez and Avilés 1977).

The decline in *P. monodon* landings between 1970–75 (Table 1) was due to political-economic conditions and not to a decline in abundance of *P. monodon*. The fishery concentrated on *P. monodon* when the industry began to market a processed product in 1976, and this accounted for peak landings of 49 729 t that year and an average effort increase to 1 329 000 BHP per fishing day (Table 1). An analysis of catch and effort data provided by the industry showed that from 1970 to 1976 there was a steady increase in catch per unit effort, but since 1977, catch has decreased while effort has continued to increase (Labra and Lederman 1980).

In 1978 landings were 29 400 t and effort was 1 700 000 BHP·d; 61% of the fleet was concentrated in 1 294 km^2 at Punta Achira Fig. 3 (Henríquez et al. 1980). The size of animals declined and the mean cephalothoracic length (CL) decreased from 39 mm in 1967 to 27 mm in 1978 as the fishery moved southward (Peñailillo 1981) (Fig. 3 and 4). Consequently in 1979 the Corporación de Fomento de la Produción (CORFO) requested IFOP to undertake an evaluation of this resource.

Low landings in 1980–82 (Fig. 1) were due to closed seasons imposed on fishing *P. monodon*; fishing for this species was only permitted as part of another fishery. Landings of *C. johni* were minimal because of low abundance. In 1983 fishing was permitted only for *P. monodon*.

The main objectives of this study are to review the present state of biological knowledge of Chilean galatheid fisheries, to outline the scientific basis for management of this resource in recent years and to discuss results of these management measures.

Research Survey Methods

This study is based on unpublished technical reports of IFOP resulting from research sponsored by the Under Secretariat of Fisheries of the Ministry of Economy, Development Corporation. Some fisheries statistics of IFOP and the National Fisheries Service have been used.

TABLE 1. Average fleet effort, catch and catch per unit of effort (CPUE) in *Pleuroncodes monodon* fisheries in Chile, 1968–78.

Years	Effort $\times 10^3$ (10^{-3} BHP^a·d)	Catch (t)	CPUE (t)
1968	0.576	9 961	17,29
1969	1.032	23 277	22,56
1970	1.257	37 678	29,97
1971	1.094	36 804	33,64
1972	0.830	32 971	39,72
1973	0.580	24 444	42,14
1974	0.723	28 305	39,15
1975	0.770	26 805	34,81
1976	1.329	49 729	36,67
1977	1.443	33 087	22,93
1978	1.700	29 403	17,30

[a] BHP (Brake Horse Power) × fishing day

The Fisheries Development Institute (IFOP) and the Catholic University of Valparaiso undertook a research survey in 1979 in the area between latitude 30°S (Coquimbo) and 38°20"S (Isla Mocha) at depths from 50 to 500 m. The main objectives of this survey were to:

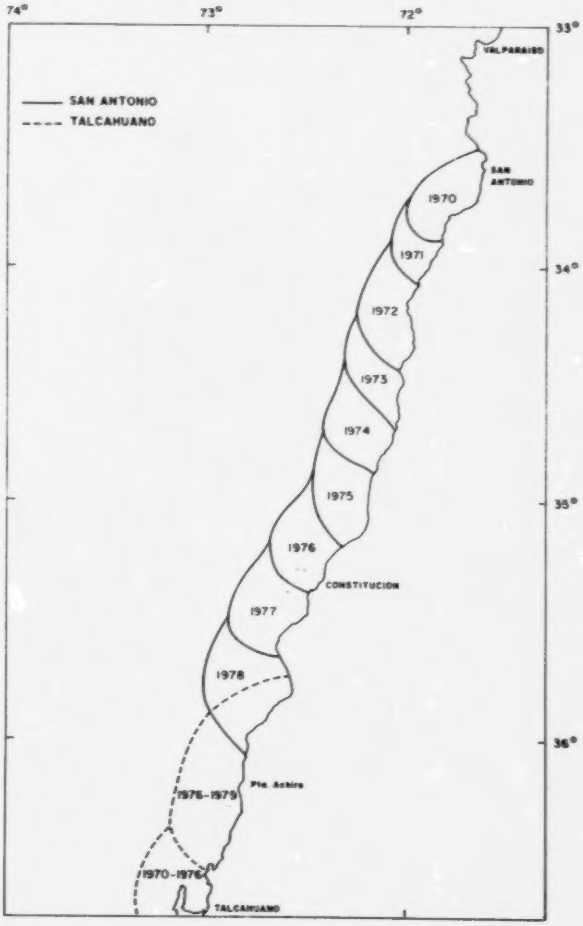

FIG. 3. Changes in fishing areas for squat lobsters in Chile (1976–79). Penailillo (1981).

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[1] Williams (1973) suggested from culture studies that these two species were actually extreme forms of one species, *M. gregaria* Fabricius (by precedence).

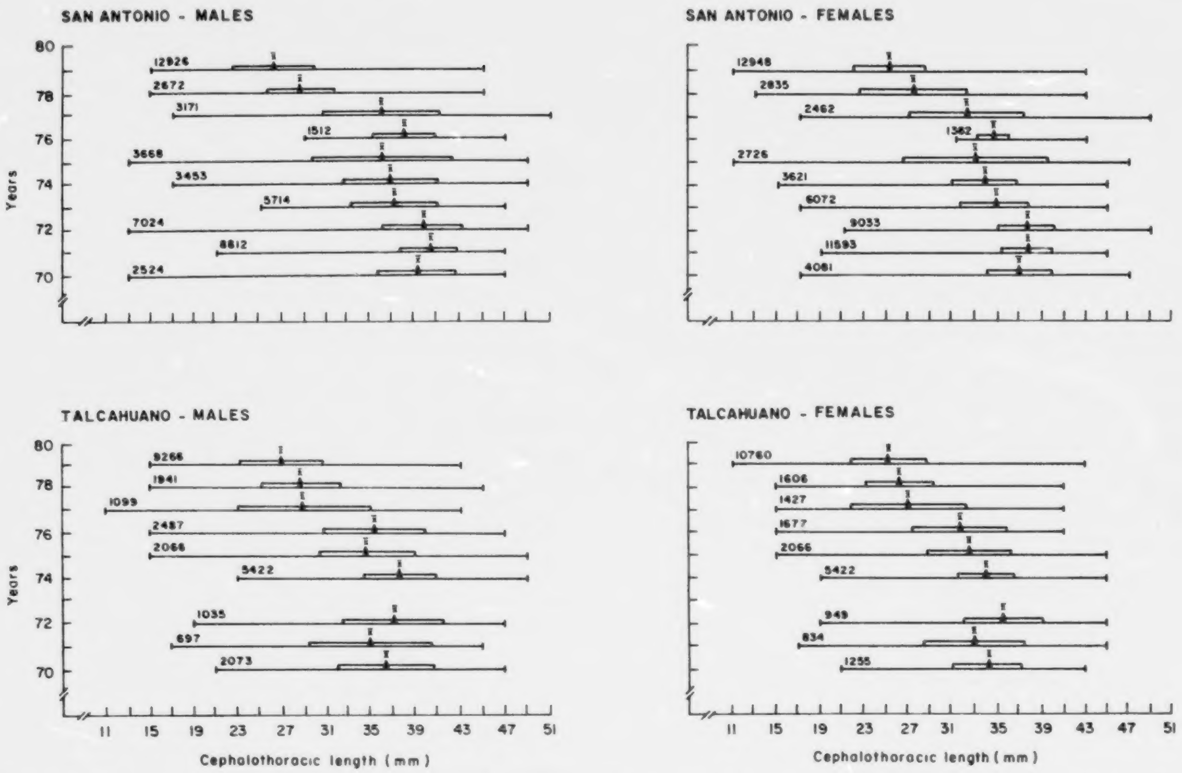

FIG. 4. Cephalothoracic length of male and female *Pleuroncodes monodon* from San Antonio and Talcahuano (1970–80). Peñaillo (1981).

(a) assess biomass of *P. monodon* in areas suitable for trawling
(b) determine oceanographic characteristics and quantify primary productivity in the area studied.

Two research vessels were used: the *B/I Carlos Porter* of IFOP, length 25.2 m, and the *Tiberiades* of the Catholic University of Valparaiso, length 19.5 m.

Random samples, stratified by depth, were taken over the entire area in the above depth range (Table 2). Table 3 shows the geographic and bathymetric distribution of squat lobsters in Chile based on results of this survey. Only *C. johni* was found in the area between 31° and 36°S but both *C. johni* and *P. monodon* were found in the area between 36° and 37°S. Further south both species virtually disappeared. Further surveys were carried out in 1980–81 using the same methods in an area extending from 35°48″S to 37°05″S at depths of 60–350 m which is the lower depth limit of *P. monodon* fishing. Surveys were repeated in 1982, 1983, and 1984 in order to locate areas of greatest abundance, estimate density, and assess size frequency distribution and biomass.

Nine stations were sampled monthly for *P. monodon* over a 12-mo period from October 1980 to September 1981 in a transect perpendicular to the coast off Punta Achira (36°13″S) at depths from 70 to 300 m with 20 to 25 minute tows using semiballoon type trawl nets (Bustos et al. 1982).

Surveys in 1979, 1980 and 1981 indicated squat lobsters were located in discrete geographic areas which were separated by areas where there were none. Random stratified sampling was planned in 1982–83 in areas where squat lobsters were concentrated; three such areas were delimited (Fig. 5):

Zone A: Punta Achira
Zone B: Cajon del Bio-Bio
Zone C: External zone of the area.

A trawl net with a 30 m head rope and a 35.4 m foot rope was used for fishing squat lobsters. The height of the mouth ranged from 2.8 to 2.4 m and the wing tips, as estimated by the method of Koyama (1974), had a mean separation of 11.25 m. Biomass was estimated by the area swept method (Alverson et al. 1964; Domain 1972; Pereyra 1967; Edwards 1968; and Kaimer et al. 1975).

TABLE 2. Position and depth of sampling stations off Chile from October, 1980 to September 1981 (Bustos et al. 1982). (*) Over Itata Shelf.

Station No.	Latitude °S	Longitude °W	Depth (m)
1	36°14′40″	72°52′40″	70
2	36°10′40″	73°00′50″	100
3	36°10′00″	73°02′50″	150
4	36°09′00″	73°04′50″	200
5	36°09′40″	73°08′30″	250
6	36°09′40″	73°15′40″	300
7*	36°08′40″	73°19′00″	200
8*	36°08′45″	73°19′00″	180
9*	36°08′45″	73°19′00″	150

TABLE 3. Geographic distribution and depth range of squat lobsters off Chile. From IFOP (1979).

		Hauls				
Depth (m)	Geographic range (latitude)	*N*	With *Cervimunida johni*	With *Pleuroncodes monodon*	Catch (t)	Density (kg·km^{-1})
	30 - 31°S	17	—	—	—	
51 - 150		10	—	—	—	
151 - 300		7	—	—	—	
	31 - 32°S	22	2	—	—	
51 - 150		6	—	—	—	
151 - 300		9	2	—	—	32.6
301 - 500		7	—	—	—	
	32 - 33°S	38	6	—	553	
51 - 150		17	—	—	—	
151 - 300		11	2	—	542.9	125
301 - 500		10	4	—	10.1	
	33 - 34°S	35	5	—	89.6	
51 - 150		24	2	—	—	
151 - 300		7	2	—	64.9	23.7
301 - 500		4	1	—	24.7	
	34 - 35°S	78	6	—	9.6	
51 - 150		15	—	—	—	
151 - 300		22	6	—	9.6	1.5
301 - 500		5	—	—	—	
	35 - 36°S	78	4	—	2.2	
51 - 150		39	2	—	0.4	
151 - 300		30	1	—	1.7	
301 - 500		9	1	—	0.1	
	36 - 37°S	96	4	40	62 125	
subzone 36°00′ - 36°30′S		40	3	21	50 758	
51 - 150		18	—	11	36 793	1,509
151 - 300		16	2	9	13 965	60
301 - 500		6	1	1	—	
subzone 36°30′ - 37°00′S		46	1	19	11 367	
51 - 150		31	—	17	11 236	663
151 - 300		12	1	2	131	65
301 - 500		3	—	—	—	
	37 - 38°S	22	1	—	—	
51 - 150		9	—	—	—	
151 - 300		8	1	—	—	61.1
301 - 500		5	—	—	—	

A 5 kg random sample was taken from the catch. Cephalothoracic length (CL) was measured from the back of the eye socket for each specimen in the sample with calipers to the nearest 0.1 mm. Animals in the samples were sorted by sex and the frequency of ovigerous females recorded. Hardness of the cephalothorax was examined to determine the time of molting. Squat lobsters were grouped into 1 mm intervals to provide a size frequency distribution of animals in 1979, 1982, and 1983. Kolmogorov-Smirnov's non-parametric test (Tate and Clelland 1957) was used to compare size distributions in these three years.

External morphology was observed to determine the sex of both *P. monodon* and *C. johni*. The male genital pore is located on the coxa of the fifth pair of walking legs, and the first two swimmeret pleopods are developed into copulating organs. The female genital pore is on the coxa of the third pair of cephalothorac legs. The first pair of swimmeret pleopods is absent. Sexual maturity and time of spawning of females were estab-

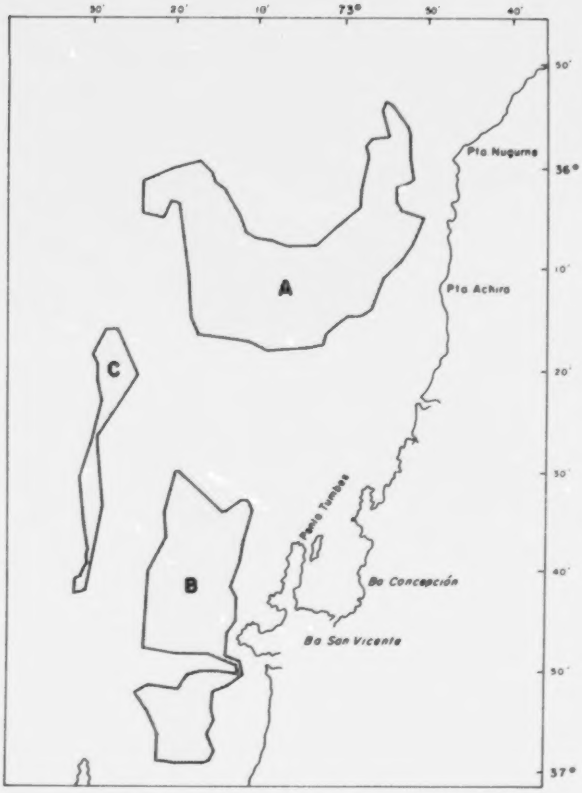

FIG. 5. Spatial boundaries of zones: A (Punta Achira), B (Cañon del Bio-Bio), and C (External).

lished from the frequency of ovigerous females in each sample.

Two methods were used to determine age and growth of *P. monodon*:

(a) Direct observations of size increases of animals kept in experimental aquaria under controlled light, temperature, salinity, oxygen and feeding conditions. Hiatt's (1948) method was used to estimate growth (Bustos et al. 1982).

(b) Statistical analysis of the length frequency distribution of CL measurements of squat lobsters using Cassie's (1954, 1963) method. The modes were determined by visual observations.

Two oceanographic cruises were carried out to determine temperature, salinity, and oxygen conditions (Fig. 6) in the fishing area, using research vessels IFOP-ECMA (Fishery Development Institute and School of Marine Science and Food), (IFOP 1979, Silva and Blanco 1980).

Results

OCEANOGRAPHY

From May 1 to June 1, 1980 the water temperature tended to be stable at depths between 100 and 200 m and ranged from 10 to 11°C except off Punta Nugurne where the temperature was over 12°C at 100 m (Fig. 6).

Salinities in the area ranged from 34.2 to 34.6‰ at the bottom, with highest salinities observed at depths of 200 m or more.

Oxygen concentrations ranged from 2 to 3 mL^{-1} in shallow water to a depth of 100 m, then decreased in deeper water to less than 1 mL^{-1} and reached a concentration of 0.5 mL^{-1} at a depth of 250 m.

The distribution of isotherms, isohalines and oxygen isolines at the bottom tended to follow the isobathic contour (Fig. 6) which according to Silva and Blanco (1980) is indicative of an absence of vertical mixing.

Subsurface equatorial water ranged from 80 to 470 m in depth on both cruises. A great part of the continental shelf and continental slope was covered by this water mass. Within this water mass, pockets of water occurred which had higher oxygen concentrations but whose volumes varied from year to year.

Intermediate antarctic water was detected below 470 m. In 1980 local upwelling was active in the vicinity of the fishing ground off Punta Nugurne (Brandhorst 1963, 1971; IFOP 1979; Silva and Blanco 1980). The absence of upwelling during the Langostino II cruise was attributed to a lack of southerly winds before and during the cruise.

Another important characteristic of the zone is that near the coast there is mixing of subantarctic water with rain and river water.

ABUNDANCE AND DISTRIBUTION

Table 4 shows estimates of squat lobster biomass for each zone from 1982 to 1983. During this period biomass increased by 5 500 t and the area occupied increased by 724 km^2. Zone A (Punta Achira) had the highest biomass in both years followed by Zones B (Cañon del Bío-Bío) and C.

Figures 7A–C show the spatial distribution of squat lobster densities in 1979, 1982, and 1983. Distribution in the last 2 years was similar. Spatial distribution by size is shown in Fig. 8.

TABLE 4. A. Total biomass (t) by zone of *Pleuroncodes monodon*.

Zone	Area (km^2)	Biomass (t)	95% confidence limits (t)
1982			
A	775 36	23 204	13 986–32 422
B	143 41	13 912	9 460–18 365
C	205 79	7 316	4 144–10 487
Total	1 124 56	44 432	33 859–55 005
1983			
A (Achira)	1 038 29	27 004	20 444–33 565
B (Bio-Bio)	639 57	21 233	14 623–27 843
C (Exterior)	170 79	1 746	947– 2 545
Total	1 848 65	49 983	40 723–59 243

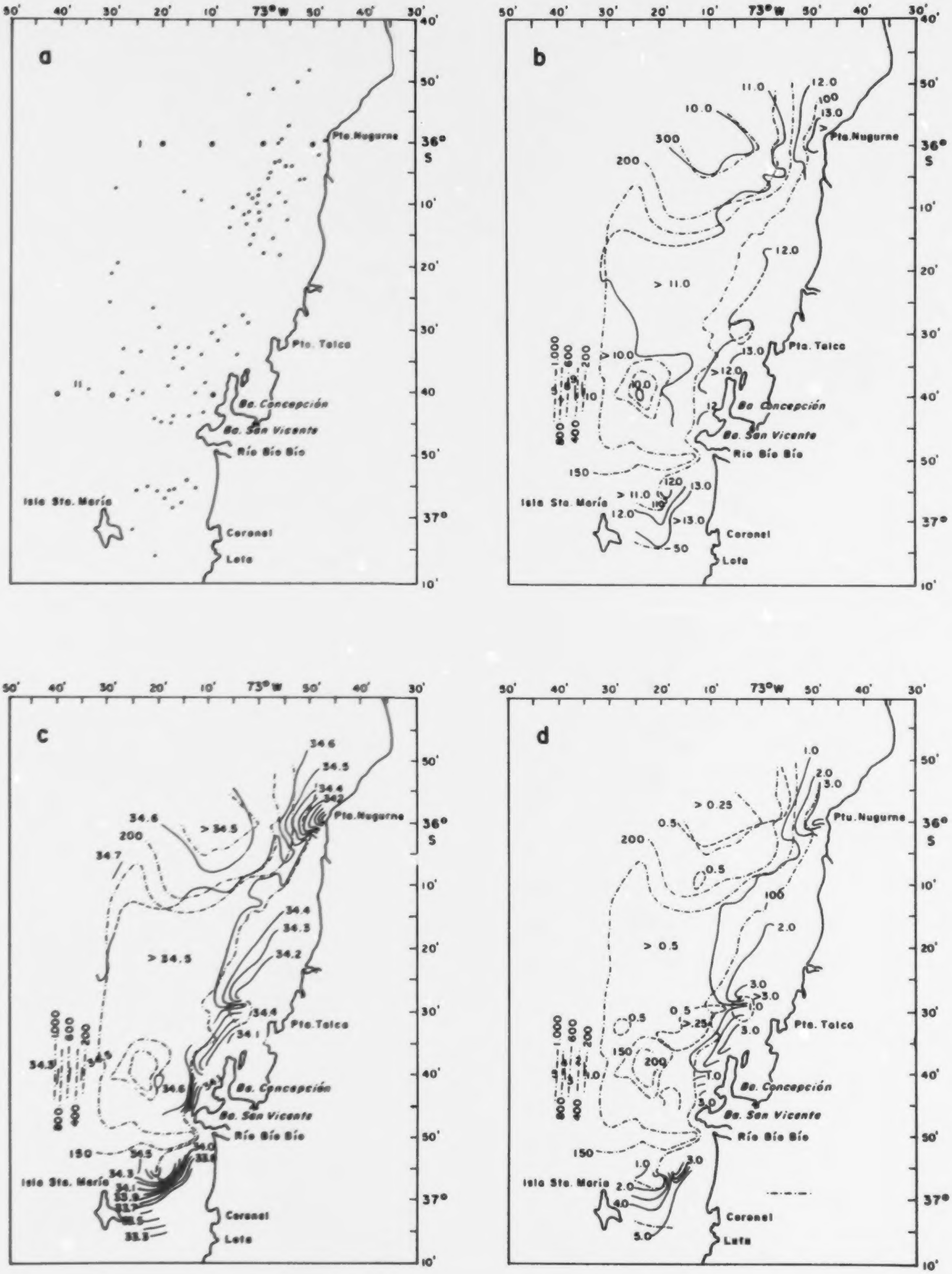
a
b
c
d
50'
40'
30'
20'
10'
73°W
36° S
37°
Pto. Nugurne
Pto. Talca
Ba. Concepción
Ba. San Vicente
Río Bío Bío
Isla Sta. María
Coronel
Lota
10.0
11.0
12.0
13.0
> 11.0
> 10.0
> 12.0
> 13.0
300
200
150
100
50
1.000
600
400
34.6
34.5
34.4
34.2
34.7
> 34.5
34.1
33.5
> 0.25
> 0.5
0.5
1.0
2.0
3.0
5.0

FIG. 6. Oceanographic conditions on squat lobster fishing grounds off Chile (Silva and Blanco, 1980). a. Oceanographic station (·); b. Depth (---) and bottom isotherms; c. Depth (---) and bottom isohalines; d. Depth (---) and bottom oxygen isolines.

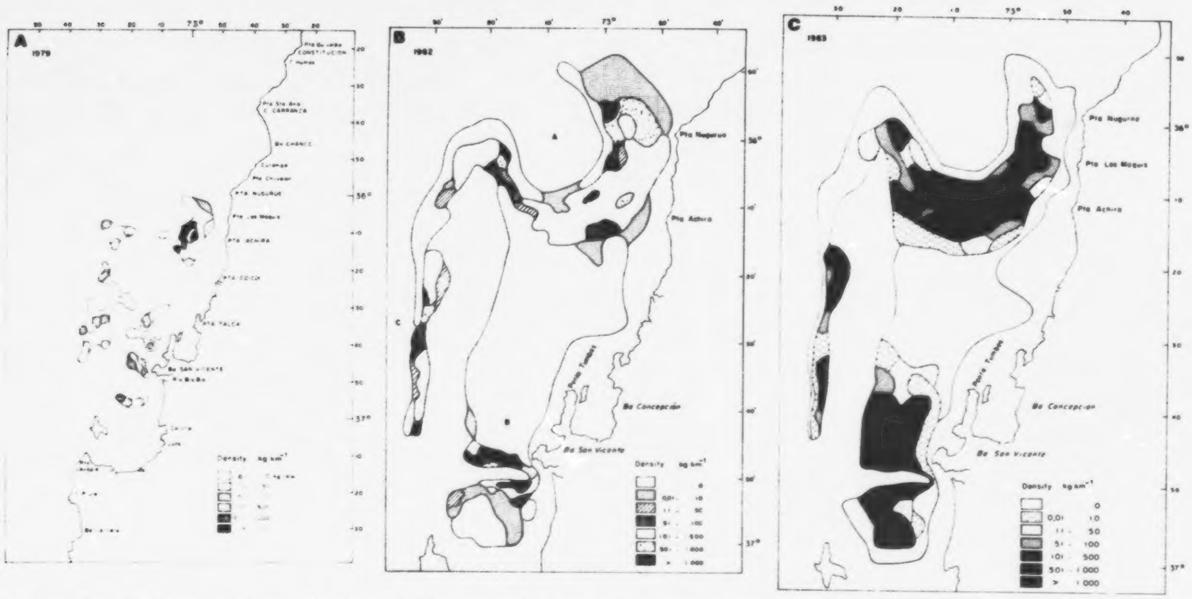
A
1979
B
1982
C
1983
73°
36°
37°
Pta Nugurne
Pta Los Maquis
Pta Achira
Ba Concepción
Ba San Vicente
Density kg·km⁻¹

FIG. 7. Density (kg·km⁻¹) distribution of *Pleuroncodes monodon* from IFOP: A. May–August, 1979. B. April 4–30, 1982. C. April–May, 1983.

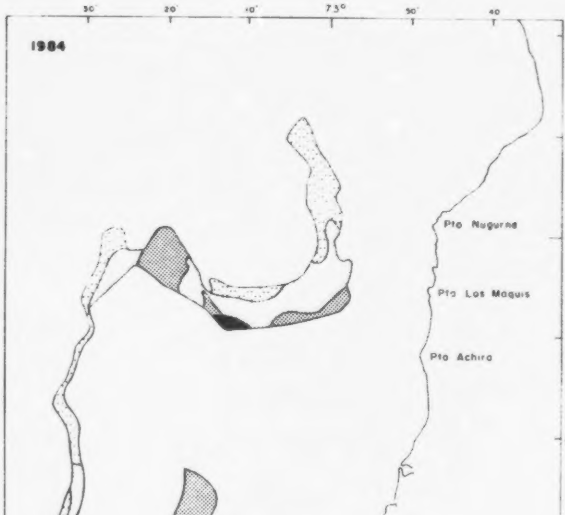
1984
30'
20'
10'
73°
50'
40'
36°
Pta Nugurne
Pta Los Maquis
Pta Achira
Ba Concepción
Ba Sn Vicente
Nº SPECIMENS / kg
0
21 - 40
41 - 80
81 - 160
161 - 320

FIG. 8. Number of animals per kilogram in catches of *Pleuroncodes monodon* (March–April 1984), from IFOP.

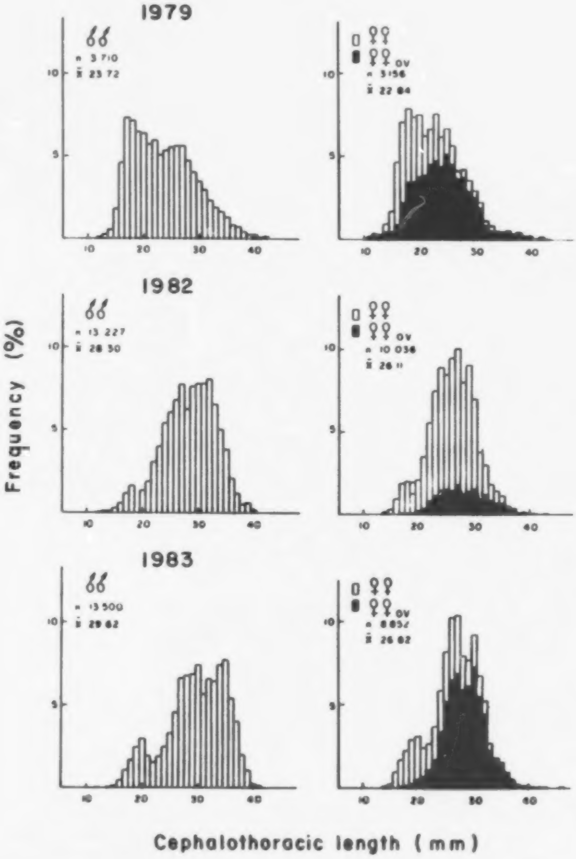

FIG. 9. Size distribution of males, females and ovigerous females of *Pleuroncodes monodon*. IFOP cruises: 1979, 1982, 1983. Table 1.

Figure 9 shows the size frequency distribution of the total *P. monodon* population on the fishing ground in 1979, 1982, and 1983. In 1979, which was the last year of non-restricted fishing, the mean size of the population was relatively low: 23.3 mm. It increased to 27.3 mm in 1982 and to 28.5 mm in 1983. A multimodal frequency distribution became more evident in 1983 along with a considerable increase in the frequency of specimens of > 30 mm CL. Size frequency distribution differed significantly ($P < 0.05$) between 1979 and 1983.

BYCATCH SPECIES

Several other species of animals were caught incidental to *P. monodon* and *C. johni* (Tables 5 and 6); these are detailed more fully in IFOP documents (Trujillo 1972; Pantoja et al. 1973; Yañez 1978; Bahamonde 1977, 1978; Labra and Lederman 1979). Table 5 estimates the amount of bycatch taken incidentally in hauls for *P. monodon* in an area from 36° to 37°S (Labra and Lederman 1979). Table 6 shows the percent distribution of the different bycatch species by zones in the Talcahuano Basin fishing area in two successive years. The most important bycatch species was *Merluccius gayi*.

Pleuroncodes and *Cervimunida* are preyed on by several species of fish (Table 7). In 1964 Henríquez and Bahamonde studied the feeding habits of *Genypterus maculatus* between San Antonio and Constitución in central Chile and reported it as an important predator on *Pleurocondes*. Of specimens of this species examined, 75% contained *Pleuroncodes*; this predator was able to consume any size of *Pleuroncodes* present. The main predators of squat lobsters appear to be *Genypterus maculatus, Paralichthys microps* and *Merluccius gayi*.

To determine whether the feeding habits of *G. maculatus* may have changed when squat lobster populations declined (Henríquez and Bahamonde 1964), further sampling was undertaken in May 1981 and results were reported by Bahamonde and Zavala (1981). It was noted that *Genypterus* was feeding mainly on *Pterygosquilla armata*. There were no squat lobsters in the stomach contents. Although both species were caught in trawl nets, they may have been spatially separated on the bottom because of different habitat preferences.

According to available information, *P. monodon* and *C. johni* are demersal, at least in the adult stage. *Pleuroncodes* is found mostly in areas of green mud that have a high organic content which according to Gallardo (1963) is probably due to the sinking of surface diatoms. These phytoplankton bloom areas may be associated with areas of upwelling that are characteristic of the central and northeast coast of Chile. Gallardo et al. (1980) found *Ampelisca araucana* zoeas and crustacean eggs in the stomachs of *P. monodon*. Diatoms (*Chaetoceros, Biddulphi, Synedra, Coscinodiscus* and *Thalassiosira*), foraminifera, bacteria filaments, organic detritus and fish scales were also found.

SPAWNING AND SPAWNING SEASON

Analysis of samples showed variation existed in the percentage of ovigerous females caught on the fishing grounds between April 6–20, 1982 and April 15–May 8, 1983; 8.1% in 1982 and 24.6% in 1983. The percentage of males was higher than females and ranged from 56 to 60%. The spawning season of *P. monodon* in the Talcahuano Basin extends from April to November. The highest frequencies of ovigerous females were recorded between June and October (Fig. 10) with percentages exceeding 25% of the total number of females. The highest percentage of females in an advanced stage of incubation was recorded in July and November. The smallest ovigerous female size observed was 9 mm CL and by 40 mm CL, most females were ovigerous (Fig. 11).

When spawning begins in April, ovigerous females are at depths between 200 and 300 m but seem to migrate to shallow waters (100–150 m) in July–August (Fig. 10) and 1979 (Fig. 11).

The spawning season of *Cervimunida* begins one month later than that of *P. monodon*, and occurs from

TABLE 5. Estimates of biomass (t) of fauna caught incidentally in *Pleuroncodes monodon* fisheries Lat. 36°–37°S, 30-min trawling, mean volocity: 2.2 knots.

	Number of tows				
	18	29	15	10	8
A. Species	51–100(m)	101–150(m)	151–200(m)	201–300(m)	301–400(m)
Merluccius gayi	714	16 167	2 562	2 264	288
Genypterus blacodes	—	—	—	43	8
Genypterus maculatus	—	82	675	47	83
Cancroids crabs	82	2 105	49	139	—
Grenadiers	—	167	1 957	24 640	4 677
Spider crab	207	—	110	1 084	1 953
Rays	—	—	113	513	1 291
Total biomass	1 003	18 532	5 468	18 730	8 300
B. Bycatch CPUE (kg km^{-1})					
Average	13	89	116	298	—
Main bycatch species	9 (*M. gayi*)	78 (*M. gayi*)	55 (*M gayi*)	233 (Grenadiers)	

Table 6. Distribution of species caught in survey cruises for squat lobsters in 1982 and 1983 off Chile expressed as a percentage of the catch by zone and total catch.

	Zone A		Zone B		Zone C			
	(Achira)		(Bio-Bio)		(Exterior)		Total	
Specie	1982	1983	1982	1983	1982	1983	1982	1983
Pleuroncodes monodon (langostino colorado)	67.99	76.13	93.94	84.95	78.86	59.18	79.46	78.64
Cervimunida johni (langostino amarillo)	1.38	0.20	—[b]	—[b]	6.15	13.30	1.61	0.8
Merluccius gayi (merluza común)	23.33	18.74	5.33	14.32	4.89	5.96	13.66	16.38
Hippoglossina macrops and *Paralichthys microps* (flatfishes)	0.68	1.76	0.01	0.25	0.43	2.37	0.39	1.21
Coelorhynchus patagoniae (grenadiers)	1.15	0.15	—[b]	—[b]	4.36	7.73	1.22	0.48
Genypterus maculatus (congrio negro)	1.48	0.64	0.18	—[a]	—[b]	—[b]	0.76	0.37
Trachurus murphyi (jurel)	3.11	1.01	0.19	0.29	5.06	5.09	2.32	0.95
Prolatilus jugularis (blanquillo)	0.01	0.44	0.05	—[a]	—[b]	—[b]	0.02	0.25
Brachyura (crabs)	0.55	0.42	0.20	0.11	0.03	—[a]	0.34	0.28
Elasmobranchii (rays and sharks)	0.16	0.34	0.02	0.04	0.22	0.32	0.12	0.22
Others	0.16	0.17	0.08	0.04	—[b]	6.05	0.10	0.42
Total	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

[a] Incidental catch
[b] No catch

Table 7. Main predators of *Pleuroncodes monodon*, between 35 and 37°S (according Melendez 1981).

Species	Predator frequency (%)	CL (mm) of squat lobsters found inside stomachs
Genypterus maculatus	25.0	2.0 - 14.0
Paralichthys microps	24.5	5.0 - 14.0
Merluccius gayi	17.4	18 - 33
Prolatilus yugularis	7.1	4 - 23
Trachurus murphyi	1.7	7.5
Coelorhynchus patagonia	0.8	7.3

May to December with >50% of observed females ovigerous from June to November. The smallest size of spawning *Cervimunida* was 25 mm CL. In 1959 the average size of ovigerous females was 35 mm, larger than that found for *Pleuroncodes* in 1980–81.

The number of eggs produced by individual *Pleuroncodes* females ranged from 3 000 to 6 000 depending on the size of the specimen. Figure 10 shows an estimated fecundity curve for this species but no attempt was made to determine whether this relationship varied over time. The fecundity of *Cervimunida* is somewhat higher, ranging from 3 400 to 6 900 eggs, again depending on the size of the animal (Alegría et al. 1963).

Population Dynamics

Analysis of data collected during 1980–81 enabled us to describe the depth distribution of squat lobsters throughout the year. In October the entire population was at a depth of 100 m and there were three distinct age groups with modes at 8, 25, and 32 mm CL. Ovigerous females of all sizes were present (Fig. 10).

During the first 2 weeks of November the population was at a depth between 70 and 100 m; at 70 m the mode was at 12 mm CL whereas at 100 m the mode was 25 mm CL, the same as observed for spawning females. The number of spawning females at 100 m was less than at 70 m, but that they were larger. There were no ovigerous females with a Cl >27 mm, but there were nonspawning females at 31–34 mm CL.

The situation was slightly different during the second fortnight of November when the population was distributed between 100–150 m depth. There were two distinct size groups at 100 m; one with a mode at 14 mm CL and another with a 25 mm CL mode. The second modal group contained the greatest number of ovigerous females. At 150 m, the dominant modal group was at 26 mm CL coinciding with the greatest number of ovigerous females.

In December the population had a greater bathymetric distribution (100–250 m); spawning had ended.

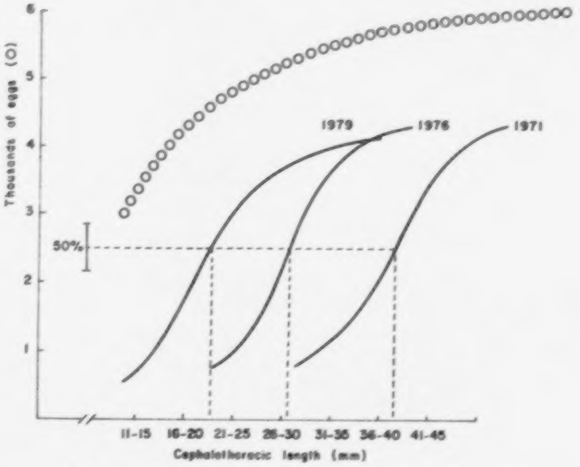

Fig. 11. Fecundity of *Pleuroncodes monodon* (0) and percentage of size distribution of ovigerous females: 1971, 1976, 1979, (IFOP), 1979.

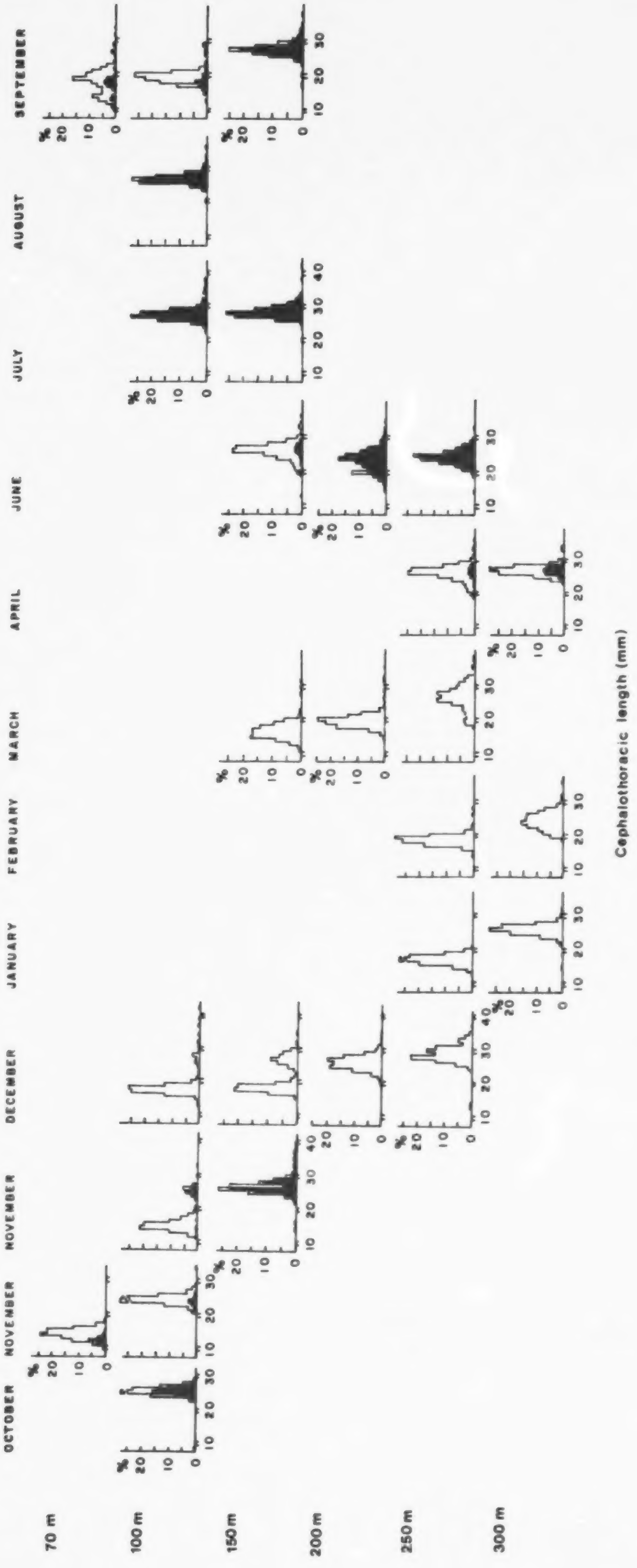

FIG. 10. *Pleuroncodes monodon*: Monthly percentage and size distribution of ovigerous females off Punta Achira (Table 2). Solid bars are ovigerous females.

There was a small mode between 13–14 mm at 250 m probably from the spawning the previous year. In January and February, the population was clearly stratified by depth between 250 and 300 m. The smallest animals were located at 250 m.

In March the population was located between 150 and 250 m. Stratification by size was obvious and the average size increased with increasing depth. In April the population was between 200 and 300 m and egg extrusion spawning had begun, the highest percentage of ovigerous females was found at 300 m.

No samples were obtained in May. In June stratification was the reverse to that noted in April. Most of the ovigerous females were between 200 and 250 m. In July and August, the population had moved upwards to depths between 100 and 150 m and showed little stratification by size.

In September the population had begun to stratify by size; the largest animals were found at 150 m, also the location of most of the ovigerous females.

Results of analysis of polymodal frequency curves of cephalothoracic lengths using Cassie's method (1954, 1963) are shown in Table 8. Estimates of the modes which were considered to be equivalent to annual year classes were made on the basis of annual surveys and these results are also included in Table 8. There were no significant differences between males and females.

As a result of experimentally raising *P. monodon* larvae it was possible to distinguish 10 stages of zoea and one stage of megalops (Bustos et al. 1982). The young measured 6 mm CL at 6 mo and 11 mm at 12 mo.

Discussion and Conclusion

Between Coquimbo (30°S) and Isla Mocha (38°20"S), *C. johni* is endemic and is distributed practically over the entire area on stoney-mud bottom. *P. monodon* has a wider but apparently more sporadic distribution and occurs at least as far north as the Peruvian coast, inhabitating muddy bottom in areas of reduced current.

The life cycle of both species is similar and they seem to have alternating periods of abundance. Publications in the first half of the 19th century refer only to *P. monodon*, and the first specimens of *C. johni* were found at the beginning of the present century. Towards 1950, *C. johni* was the only species of squat lobster exploited in the fishery, but it has gradually been replaced by *P. monodon* in recent years. In the last 7 yr the fishery for this species has moved southward and is now in a well defined fishing area in the Talcahuano Basin (Fig. 3).

TABLE 8. Average size (CL) by age class of *Pleuroncodes monodon* calculated according to Cassie's method for samples of Punta Achira (1980–81).

	Average CL size (Cassie)		Average size estimated from
Age (y)	Males	Females	survey data modes
0	11.00	11.3	
1	15.10	15.0	16.60
2	20.20	19.1	24.70
3	27.40	24.0	29.80
4	32.20	37.6	36.40
5	35.20	36.2	41.00
6	38.80	39.2	

Both species *C. johni* and *P. monodon* feed on detritus and the remains of marine organisms. They are preyed upon by several species of fish, some of which are commercially important.

Populations of both species seem to be regulated by both environmental factors and commercial fisheries. In recent years population decreases have been attributed to fishing but there is evidence that natural phenomena may also be important. A large part of the detritus on which squat lobsters feed is produced in the photic zone of subantarctic water (Gallardo et al. 1980). Accumulation of detritus depends on upwelling which occurs in the vicinity of the present fishing grounds off Punta Nugurne (Brandhorst 1963; Kelly and Blanco 1984). Also, in recent years clupeid fisheries have increased in both the north and central southern area, including Talcahuano. Clupeids are large consumers of plankton, especially phytoplankton, and this may affect the food supply for bentho-demersal detritus eating animals.

There are other factors related to detritus production that merit investigation: variation in the transport of detritus by rivers and the dynamics of the subsurface equatorial water mass that is dragged southward by the Gunther Current. This water mass has a high salinity and low oxygen content (Brandhorst 1963; and Robles et al. 1976) and expands over the upper slope of the continental shelf. This may explain the absence of demersal fisheries in the northern zone (Robles et al. 1976). Squat lobsters may live at the boundary of these water masses and movement of *Pleuroncodes* populations may be due to the dynamic interaction between them.

At present, there is insufficient oceanographic data to explain many of the biological phenomenon observed with squat lobsters. Collection of oceanographic data in conjunction with squat lobster abundance and distribution should have a high priority.

Acknowledgments

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Interactions Between Norway Lobster (*Nephrops norvegicus*) and Cod (*Gadus morhua*) and their Fisheries in the Irish Sea

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BRANDER, K. M., AND D. B. BENNETT. 1986. Interactions between Norway lobster (*Nephrops norvegicus*) and cod (*Gadus morhua*) and their fisheries in the Irish Sea, p. 269–281. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

A multispecies steady state model of the technical (by-catch) and biological (predation) interactions between Norway lobster (*Nephrops norvegicus*) and cod (*Gadus morhua*) in the Irish Sea has been constructed and gives a consistent and apparently sensible representation of their joint response to different levels of exploitation. The model, which is age structured and incorporates growth, mortality, maturity, stock/recruit relationship, selectivity, by-catch levels, discarding, predation, and unit value, was found to be robust to changes in the inputs for which most uncertainty exists, e.g. the cod stock/recruit and the functional feeding relationships. By demonstrating model sensitivity to poorly estimated but important parameters attention has been focussed on the kind of work needed to increase confidence in the use of the model for determining management strategy. The model allows direct comparison between the multispecies approach and the traditional single species yield per recruit model, and casts serious doubts on the existing management strategy. With the inclusion of predation on *Nephrops*, which is a function of cod biomass, the model suggests that, if the objective were to be to increase the joint value of the two species, then fishing mortality should be reduced on *Nephrops*, but increased on cod.

Un modèle à l'équilibre multispécifique des interactions techniques (prises occasionnelles) et biologiques (prédation) entre la langoustine (*Nephrops norvegicus*) et la morue (*Gadus morhua*) dans la mer d'Irlande a été élaboré. Il représente de façon cohérente et sensible la réaction de ces deux espèces à divers niveaux d'exploitation. Le modèle, qui est structuré par âges et tient compte de la croissance, de la mortalité, de la maturité, de la relation stock-recrutement, de la sélectivité, du niveau des prises occasionnelles, du rejet de prises, de la prédation et de la valeur unitaire réagit bien aux variations des paramètres d'entrée présentant le plus d'incertitude, par exemple, la relation stock-recrue chez la morue et les relations fonctionnelles d'alimentation. Le fait que le modèle soit sensible à des paramètres mal estimés mais importants a permis de mettre l'accent sur le type de travaux nécessaires pour en accroître la fiabilité quand il est appliqué à la détermination d'une stratégie de gestion. Le modèle permet de comparer directement l'approche multispécifique à l'approche mono-spécifique du modèle du rendement par recrue et soulève des doutes sérieux quant à la pertinence de la stratégie de gestion actuelle. L'inclusion au modèle du paramètre de la prédation de *Nephrops*, qui est fonction de la biomasse de la morue, indique qu'il faudrait réduire la mortalité par la pêche de *Nephrops* et accroître celle de la morue pour augmenter la valeur globale des deux espèces.

Introduction

Understanding the interactions between species and between fisheries (biological and technical interactions) is widely perceived as being of critical importance to the achievement of fisheries management goals (e.g. Rothschild 1983). Several recent studies have developed multispecies approaches to take account of feeding relationships (e.g. Majkowski 1981; Pope and Knights 1982) and technical interactions (e.g. Murawski 1984). The case for applying such models to stocks in the Irish Sea was made by Brander (1981).

The Irish Sea (ICES Division VIIa) is unusual in that the most important directed trawl fishery is for the crustacean *Nephrops norvegicus* (L.) or Norway lobster. Average annual international landings of the species for 1978–82 were 8 700 t, compared with 10 700 t of cod (*Gadus morhua* L.) and 13 700 t of whiting (*Merlangius merlangus* (L.)), but the unit value of *Nephrops* is four times that of whiting and twice that of cod. In value, *Nephrops* and cod are therefore the two main species landed from the Irish Sea. Because cod is a major predator on *Nephrops* and because the fisheries directed at each of the species also catch the other as a by-catch, a model incorporating these biological and technical interactions is needed in order to evaluate the consequences of various possible management strategies for the two species.

Of course cod is not the only predator on *Nephrops*, nor is *Nephrops* the only prey of cod, but extensive sampling of the principal fish species which occur on *Nephrops* grounds in the western Irish Sea shows that cod is by far the most important predator (Symonds and Elson 1983), accounting for 88% of the total quantity (weight) of *Nephrops* eaten. By restricting the model to only two species it remains tractable and can be used to address questions of management strategy in the two major fisheries.

The distribution of *Nephrops* in the Irish Sea is restricted to two large areas of muddy substrate, one in the northwest corner, between the Isle of Man and the Northern Irish coast, and the other off the Cumbrian coast of England (Fig. 1). The former is much more extensive and accounts for 88% of the total landings. The model treats the Irish Sea *Nephrops* stock as a single unit and similarly the cod stock is treated as one unit (as it is in all stock assessments to date).

Having specified that the problem to be tackled is an evaluation of the consequences of various possible management strategies for the two species, the model chosen to carry this out is one developed by Shepherd (1984). This is a simple extension of the standard yield per recruit model, which sums annual numbers and weights at age. It includes a stock–recruit (S/R) relationship (Shepherd 1982), inter- and intra-specific predation and technical interactions between fisheries. The model can be set to give constant recruitment and no biological or technical interactions and so reproduce exactly the single species yield per recruit calculations on which current management strategy is based. In this way the effect of incorporating any of these factors can be compared directly with results of current yield per recruit methods. The reasons for using this kind of simplified steady state approach are discussed more fully by Shepherd (1984) and he describes the model in detail and points out the limitations and possible further developments.

There is sometimes uneasiness about applying models to situations which are not well understood and for which information is incomplete or subject to uncertainty. This unease is understandable if the results of a complex and opaque model are applied uncritically. Although our knowledge of several aspects of the dynamics of these species is at a rudimentary stage, a number of arguments can be put forward to justify the modelling approach adopted here:

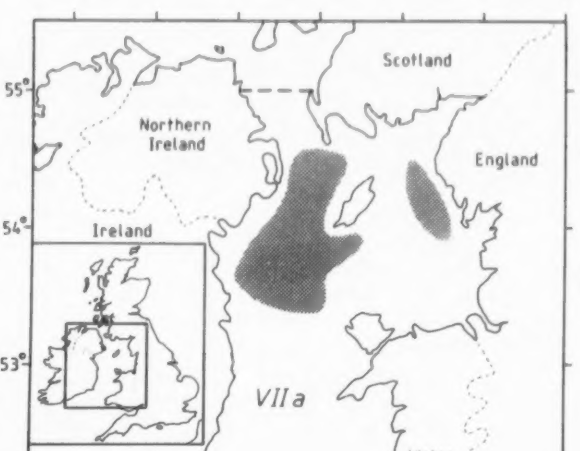

FIG. 1. *Nephrops* fishing grounds in the Irish Sea, ICES Division VIIA.

1) Yield per recruit models are already being used to determine long term strategy for managing one of the stocks (cod), even though the assumption that recruitment is independent of parent stock level is untenable over the full range of stock size and uncertain even over a limited range close to the present level. Until the consequences of incorporating S/R and biological and technical interactions have been explored, we do not know how big an effect they might have on the long term strategy for these two stocks. Even if the only consequence of this modelling exercise is to instil caution in the application of the results from single species yield per recruit models, it will have been worthwhile.

2) Once we have seen which factors have an important effect and which have a small effect, the experimental and field work can be guided to address the uncertainties which matter most.

3) By applying the present model it may become apparent that the representation of some of the processes is inappropriate and therefore potentially misleading. For example Shepherd (1984) has pointed out that the functional form used to represent predation is likely to be misleading at very high prey biomass levels. This is not just a problem "within the model", but points to a genuine difficulty in describing the relationship between predator and prey. A minor alteration to Shepherd's form of the feeding equation is described later.

The Model

DESCRIPTION OF THE MODEL

The model uses standard yield per recruit calculation — summing the products of number-at-age and weight-at-age to give stock biomass — and this part of the model needs no description. Figure 2 is a schematic representation of the significant biological and technical interactions considered in the application of the model.

The instantaneous rate at which cod eat *Nephrops* is governed by the biomass of cod and by a size preference function. The two fisheries use different mesh sizes; 70 mm in the cod-directed fishery and 55 mm in the *Nephrops*-directed fishery. Each fishery therefore has its own selection and discard characteristics and each generates different proportions of mortality on the two species. In order to consider joint management strategies for the two fisheries the unit value of each is used, since it makes little sense to add together weights, which represent very different monetary values.

The calculation of steady state yield, biomass, recruitment and value of each species and of the two species added together in each fishery and in the two fisheries added together is carried out for a range of values of fishing mortality. First fishing mortalities on each age of each species in each fishery are calculated and added to the basal natural mortality and to the predation mortality on each age. The basal natural mortality is the natural mortality due to causes other than predation. These mortalities are then used in conven-

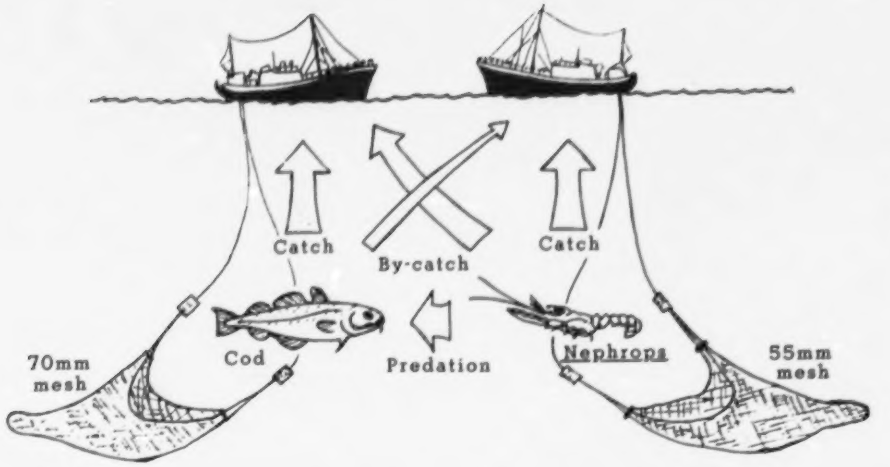

FIG. 2. Schematic representation of the biological and technical interactions between *Nephrops* and cod.

tional yield per recruit calculations, which are combined with the stock recruit relationship to give absolute biomasses and yields. As well as tables of yield, biomass, recruitment and value for all selected combinations of fishing mortality in the two fisheries, the predation mortality on each age and the total weight of prey consumed is printed out.

INPUT VALUES

The complete input file for the "standard run" (Run 1) is given in Table 1. Sources of the values used and choice of particular levels are detailed below. All biomass figures are for 1 January.

Cod Population Parameters

The 1982 weight-at-age data from the ICES Irish Sea Working Group Report (Anon. 1983) were used to express growth rate (extrapolated for ages 8 to 10 years) (Fig. 3). The proportion mature-at-age (Fig. 3) was taken from the same source. Natural mortality for Irish Sea cod was estimated as 0.2 (Brander 1975) using results from cohort analysis and tagging experiments. Values of spawning stock and recruitment estimated by virtual population analysis (VPA) (Anon. 1983) are given in Fig. 4. Spawning biomass has been corrected to 1 January and recruitment is given as 0-group on 1 January. They show no obvious relationship, but the highest values of recruitment occur at the lowest spawning stock levels recorded and the lowest at the highest stock levels, suggesting some over compensation. The "standard run" therefore uses a slightly domed relationship by inserting a value of $\beta = 2$ in the equation $R = aB/[1 + (B/K)^{\beta}]$ proposed by Shepherd (1982). The maximum recruitment per unit of biomass (a) is estimated from the data as 2 recruits/kg. The "threshold biomass" parameter (K) is set so that the curve passes through the joint mean of recruitment and spawning stock biomass. Because the shape of the stock recruit relationship is uncertain and because it may have an important effect on overall results, alternative values of β have been substituted in later runs (Runs 3 and 4). Values of $\beta = 1$, which gives an asymptotic "Beverton and Holt" type of curve and $\beta = 5$, which is very domed, were used and the K values were also adjusted so that the curves (which are shown in Fig. 4) pass through the joint mean.

The value per tonne (£386) of cod used in the model is the 1982 first-sale value for Northern Ireland, where much of the cod and most of the *Nephrops* are landed. The permitted mesh size in the cod-directed fishery is 70 mm. The mean selection length is 25 cm (≃170 g) (Macer 1982) and consequently 0-group cod are not selected but all others are fully selected. However, 1-yr olds are only large enough to be fully exploited in the last quarter of the year, and consequently their selec-

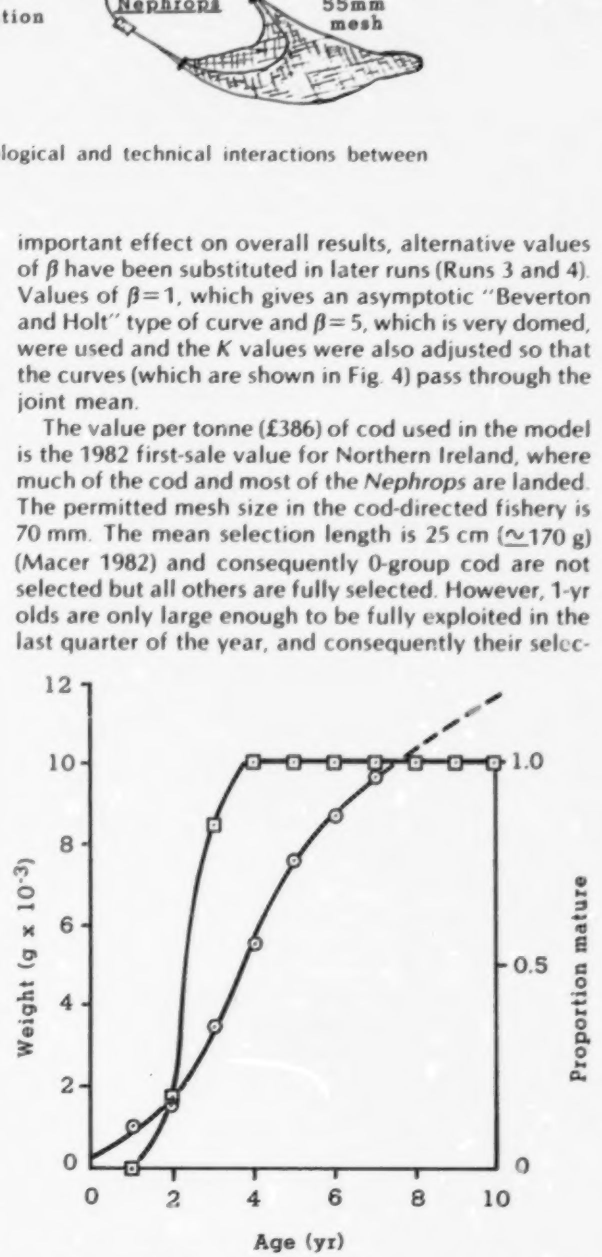

FIG. 3. Growth (O) and maturity (□) of cod, derived from Anon. (1983).

TABLE 1. The complete input file for the "standard run"

```
IRISH SEA COD NEPHROPS INTERACTION (70-55MM MESH)
2 SPECIES
1 PREDATOR
COD
10 .2 (OLDEST AGE & NATURAL MORTALITY)
0 0 .17 .85 1 1 1 1 1 1 1 (FRACTION MATURE)
33 1010 1530 3490 5560 7590 8700 9650 10400 11050 11700 (STOCK WEIGHT AT AGE)
.002 7.70E9 2 (STOCK RECRUITMENT RELATIONSHIP-A,K,BETA)
1E-3 1 .1E-10 6E-1 (PREY PREFERENCE-SIZE,GSD,MORTALITY PER GRAM,MIN PREY)
NEPHROPS
10 .1 (OLDEST AGE & NATURAL MORTALITY)
0 0 .1 .5 .8 .95 1 1 1 1 1 (FRACTION MATURE)
.004 .50 1.86 3.28 4.93 6.92 9.16 11.8 14.3 17.1 19.4 (STOCK WEIGHT AT AGE)
100 2.00E7 1 (STOCK RECRUITMENT RELATIONSHIP-A,K,BETA)
0,1 (PREDATION PREFERENCE MATRIX)
2 FISHERIES
COD DIRECTED (70MM MESH)
COD DATA
386 £/TONNE (UNIT VALUE)
33 1010 1530 3490 5560 7590 8700 9650 10400 11050 11700 (CATCH WEIGHT AT AGE)
0 .25 1 1 1 1 1 1 1 1 1 (FRACTION SELECTED)
1 .5 .1 0 0 0 0 0 0 0 0 (FRACTION DISCARDED)
NEPHROPS DATA
2333 £/TONNE (UNIT VALUE)
.004 .50 1.86 3.28 4.93 6.92 9.16 11.8 14.3 17.1 19.4 (CATCH WEIGHT AT AGE)
0 .02 .04 .06 .07 .08 .09 .09 .09 .09 .1 (FRACTION SELECTED)
1 .94 .74 .36 .16 .08 .02 .01 0 0 0 (FRACTION DISCARDED)
NEPHROPS DIRECTED (55MM MESH)
COD DATA
386 £/TONNE (UNIT VALUE)
33 1010 1530 3490 5560 7590 8700 9650 10400 11050 11700 (CATCH WEIGHT AT AGE)
.1 .2 .2 .2 .2 .2 .2 .2 .2 .2 .2 (FRACTION SELECTED)
1 .5 .1 0 0 0 0 0 0 0 0 (FRACTION DISCARDED)
NEPHROPS DATA
2333 £/TONNE (UNIT VALUE)
.004 .50 1.86 3.28 4.93 6.92 9.16 11.8 14.3 17.1 19.4 (CATCH WEIGHT AT AGE)
.01 .28 .77 .93 .97 .99 .99 1 1 1 1 (FRACTION SELECTED)
1 .94 .74 .36 .16 .08 .02 .01 0 0 0 (FRACTION DISCARDED)
```

tion was reduced to 0.25 (Fig. 5). The pattern of cod discarding (Fig. 5) has been set to take account of the minimum landing size of 30 cm, which is increased to 45 cm in the last quarter of the year. Where cod are a by-catch in the 55 mm mesh *Nephrops*-directed fishery the cod discarding (Fig. 5) was assumed to be the same as in the cod-directed fishery, while the selection (Fig. 5) takes account of the smaller mesh used and assumes that only 20% of the *Nephrops*-directed fishing mortality is applied to cod as a by-catch. The relative mortality generated on *Nephrops* and cod in the different fisheries is being investigated further at present. Discarded fish are assumed to be dead.

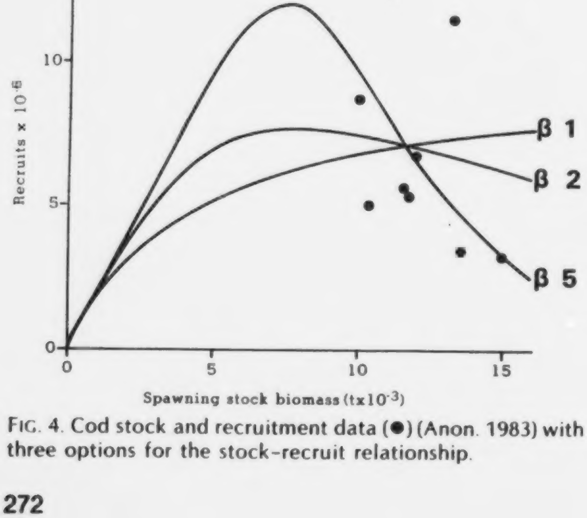

FIG. 4. Cod stock and recruitment data (●) (Anon. 1983) with three options for the stock-recruit relationship.

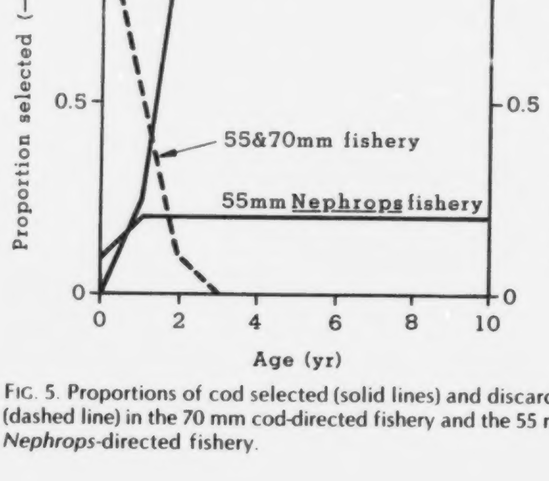

FIG. 5. Proportions of cod selected (solid lines) and discarded (dashed line) in the 70 mm cod-directed fishery and the 55 mm *Nephrops*-directed fishery.

Nephrops *Population Parameters*

Nephrops in the Irish Sea are landed as tails. Growth has therefore been expressed as weight (g) of tails, which is approximately a third of the whole weight. Growth data for the Irish Sea (Farmer 1973; Hillis 1979) indicate different growth rates for males and females (Fig. 6), and a combined sex growth curve, assuming a 50:50 sex ratio, has been derived. The maturity ogive (Fig. 7) was calculated using a minimum size at first maturity of 20 mm carapace length (CL) (Farmer 1975), 100% maturity at 29 mm (Thomas 1964), and assuming an interquartile range of 3 mm. Basal natural mortality has been assumed to be $M=0.1$. Where the model has been run with constant natural mortality (Run 2) a value of $M=0.3$ was used, which incorporates a fixed predation mortality. The stock-recruit relationship for *Nephrops* has been set to give virtually constant recruitment at all stock levels (Fig. 8), since we have no data to suggest otherwise. The choice of the threshold biomass (K) of Shepherd's equation, which governs the level of recruitment, is discussed below.

The tail weight value per tonne (£2333) of *Nephrops* is the 1982 first-sale value for Northern Ireland, where most of the *Nephrops* are landed. Previous single species *Nephrops* assessments (Anon. 1978, 1979) have used a range of values for the selection factor and also the selection range, because of uncertainties regarding *Nephrops* mesh selection. Following a review of selection results for the Irish Sea (Bennett 1984) the following values for cod-end selection were used in a logistic function to produce selection ogives (Fig. 9 and 10):

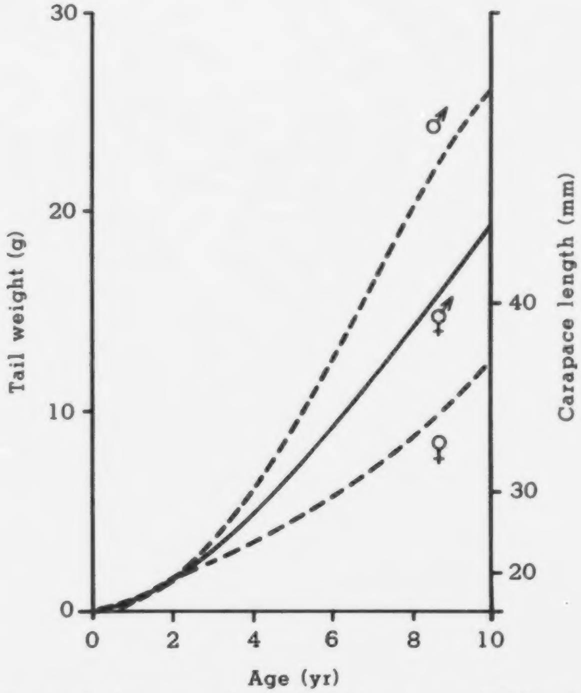

FIG. 6. *Nephrops* growth, derived from Farmer (1973) and Hillis (1979).

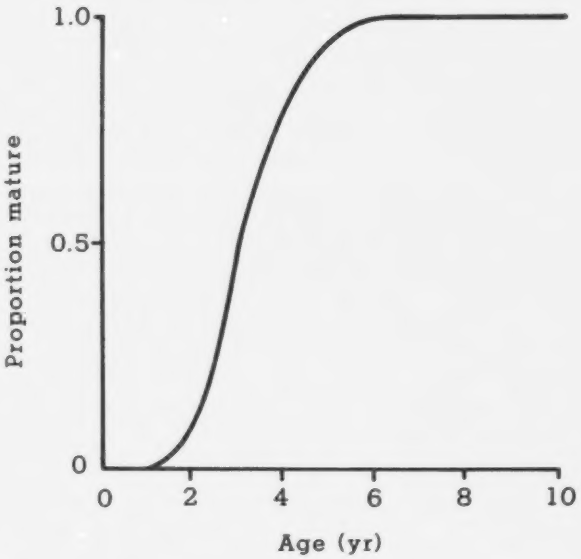

FIG. 7. Maturity ogive for *Nephrops*.

Mesh size (mm)	Selection factor	Selection range (mm CL)
55	0.31	7.1
60	0.32	10.0
70	0.33	12.5

Although the permissible mesh when fishing for *Nephrops* is 60 mm, it is considered that 55 mm is a more realistic estimate of the mesh size actually in use. Discard observations were available for the period 1980–82 from Northern Ireland (R. P. Briggs, pers comm). The discard length compositions available for males and females were combined assuming a 50:50 sex

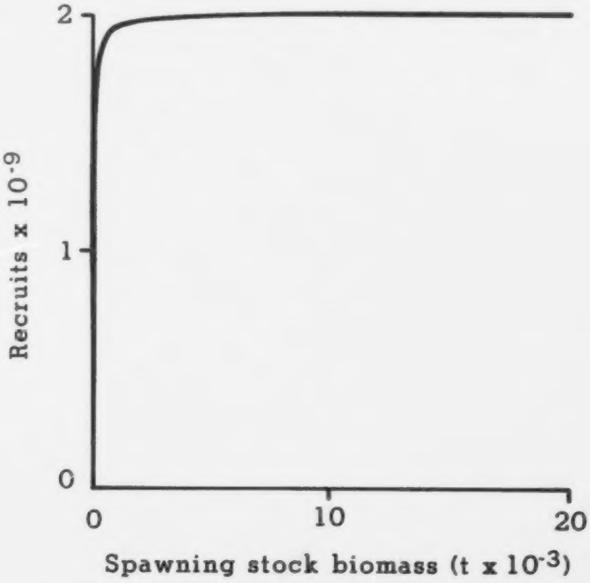

FIG. 8. Stock-recruitment relationship for *Nephrops*.

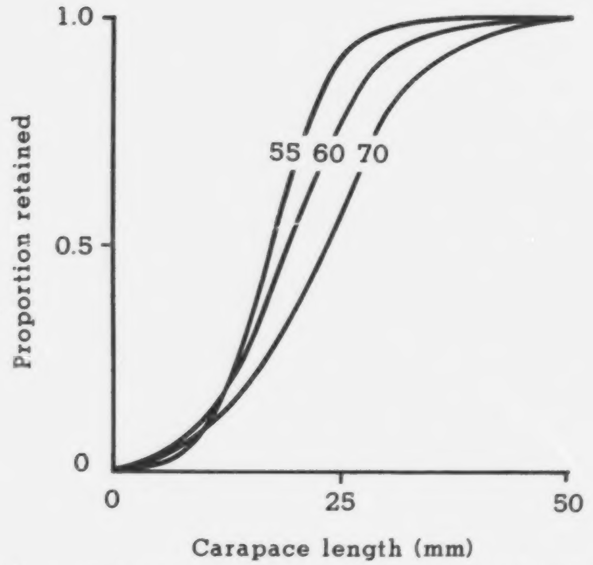

FIG. 9. *Nephrops* cod-end mesh selection ogives for three mesh sizes (55, 60, 70 mm).

ratio and converted to age (Fig. 10) using the combined sex growth data (Fig. 6). The selection of *Nephrops* in the 70 mm cod-directed fishery was estimated for 70 mm mesh (Fig. 9) and it was assumed that only 10% of the cod-directed fishing mortality is applied to *Nephrops* as a by-catch. Discarding in the 70 mm fishery was considered to be the same as in the 55 mm *Nephrops*-directed fishery.

Predation Mortality and the Functional Feeding Relationship

Two aspects of feeding need to be taken into account: the overall level of predation mortality and the relative level which falls on each prey age-group. These are adjusted respectively by the mortality per gram and the preferred prey size parameters of the functional feeding relationship (FFR). The mortality per gram is simply the instantaneous coefficient of predation mortality generated annually by each gram of predator stock biomass. Full details of the FFR and the reasons for using it are given by Shepherd (1984).

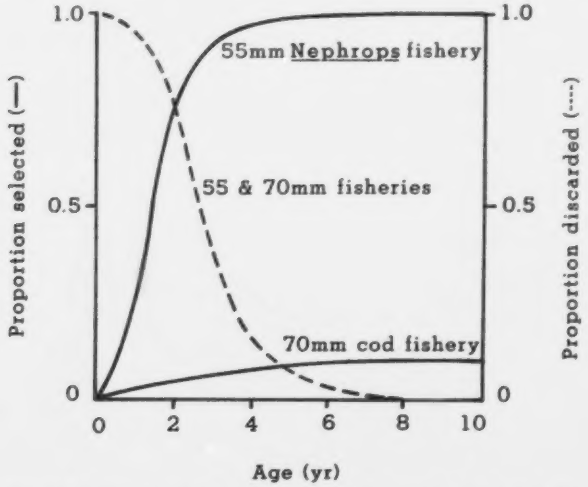

FIG. 10. Proportions of *Nephrops* selected (solid lines) and discarded (dashed line) in the 55 mm *Nephrops*-directed fishery and the 70 mm cod-directed fishery.

A number of recent studies of predation on *Nephrops* in the Irish Sea provide information which can be used to obtain values for input parameters of the FFR (Armstrong 1979, 1982; Brander 1981; Fannon and Hillis 1982; Boyd 1983; Patterson 1983; Symonds and Elson 1983). An unpublished estimate of total consumption of *Nephrops* by Brander, based on the work of Armstrong (1979) and quoted by the ICES *Nephrops* Working Group (Anon. 1982) gave a range of 3100–3900 t whole weight (1033–1300 t tail weight) of *Nephrops* consumed by cod in 1978. The estimate of total consumption by Fannon and Hillis (1982) lies within the same range.

There are however two major problems with these and other estimates: (1) The method of calculating total consumption from observed stomach contents can give rise to variations of a factor of two or more, depending on which empirical feeding model is applied (Daan 1973; Jones 1974a). Further experimental work is being planned to look at the gastric evacuation time for *Nephrops* by cod. (2) We have estimates of consumption of *Nephrops* by cod in areas where *Nephrops* occur, but the fraction of the cod stock which is not in *Nephrops* areas and therefore not feeding on *Nephrops* has to be estimated as well, since we are including the whole of the Irish Sea cod biomass in our model. The estimate of the proportion of the cod stock which is feeding on *Nephrops* throughout the year is made by comparing the known distribution of the *Nephrops* population, as shown from fishing surveys and sediment charts, with the distribution of the cod stock as deduced from rectangle charts of commercial catch per unit of effort by season. The resulting estimate, that 20–25% of the cod stock is feeding on *Nephrops*, is not a very reliable one and the consequences of a higher value (it is unlikely to be lower) need to be explored.

The FFR causes the mortality due to a particular size (weight) of predator to be log-normally distributed about a preferred prey weight. Detailed studies of the size composition of *Nephrops* in cod stomachs (Armstrong 1979; Boyd 1983; unpublished data) show that this is a good representation of what actually happens and that the preferred size (in *Nephrops* tail weight) is 1% of cod body weight. Detailed studies also show that cod rarely feed on *Nephrops* below 13 mm carapace length (≃0.6 g tail weight) and so the original FFR (Shepherd 1984) has been truncated below this size. The effect of this in the model is to eliminate predation mortality by cod on 0- and 1-group *Nephrops*.

SETTING UP THE "STANDARD RUN" AND CHECKING FOR SELF CONSISTENCY

The usual procedure in mathematical modeling is to set up the model, put in the best estimates of the parameters and then validate, by comparing the results with the "real world". In the previous section we discussed the sources of parameter values used for the "standard run" and in this section we go on to compare results from the "standard run" with observed values. This procedure cannot be strictly described as a validation of the model, however, because many of the observed values were used in estimating input parameters and the process is therefore circular. In two cases the input parameters were obtained by iteratively tuning the model to give particular output values. The two parameters in question are the input value of mortality per gram in the feeding relationship and the level of *K* (threshold biomass) in the *Nephrops* stock/recruit relationship. In the former case a mortality of $0.1 \times 10^{-10} g^{-1}$ of cod results in 1544 t (tail weight) of *Nephrops* being consumed, which is slightly above consumption estimates quoted previously. As was pointed out, these probably err on the low side. In the latter case the level of *Nephrops* recruitment was adjusted to bring the resultant spawning stock biomass (SSB) close to the value estimated by the *Nephrops* larvae survey (Nichols et al. 1983) of 9490 t tail weight. A *K* value of 2×10^7 g gave a SSB of 9670 t from the "standard run".

This completes the discussion of the parameter values used in the "standard run" and given in Table 1. We can now go on to check that the output from this run is fully self consistent and satisfies our estimates of cod and *Nephrops* biomass, recruitment and yield. Values of all these are calculated for a range of levels of fishing mortality (F) in each fishery. Figure 11d, for example, shows the biomass of *Nephrops* contoured for a range of *F* values from 0 to 1 in steps of 0.1. The biomass of *Nephrops* declines fairly quickly as *F* increases in the *Nephrops* fishery, but *Nephrops* biomass increases as *F* increases in the cod fishery. In order to check that the output is consistent with our estimate of *Nephrops* biomass from the larvae surveys (9490 t) we obviously have to decide what combination of *F* values for the two fisheries is acting at present. The virtual population analysis for cod (Anon. 1983) gives a mean value of $F = 0.6$ over recent years. For *Nephrops* the total mortality (*Z*) can be estimated as 0.6, using length cohort analysis (Jones 1974b) based on the Northern Ireland catch length composition of males and females separately for 1980–82 (R. P. Briggs, pers. comm.) For the female length composition this estimate of total mortality is virtually independent of the natural mortality (*M*) value assumed to begin with, but for males it is somewhat variable, being closest to $Z = 0.6$ when the input *M* value is 0.3. This is consistent with output from the model, which shows that the observed SSB of 9490 t occurs at an *F* of slightly more than 0.3 on *Nephrops*.

Table 2 shows the output values of biomass, recruitment and yield of cod and *Nephrops* from the "standard run" ($F_{COD} = 0.6$ and $F_{NEP} = 0.3$) and the independent

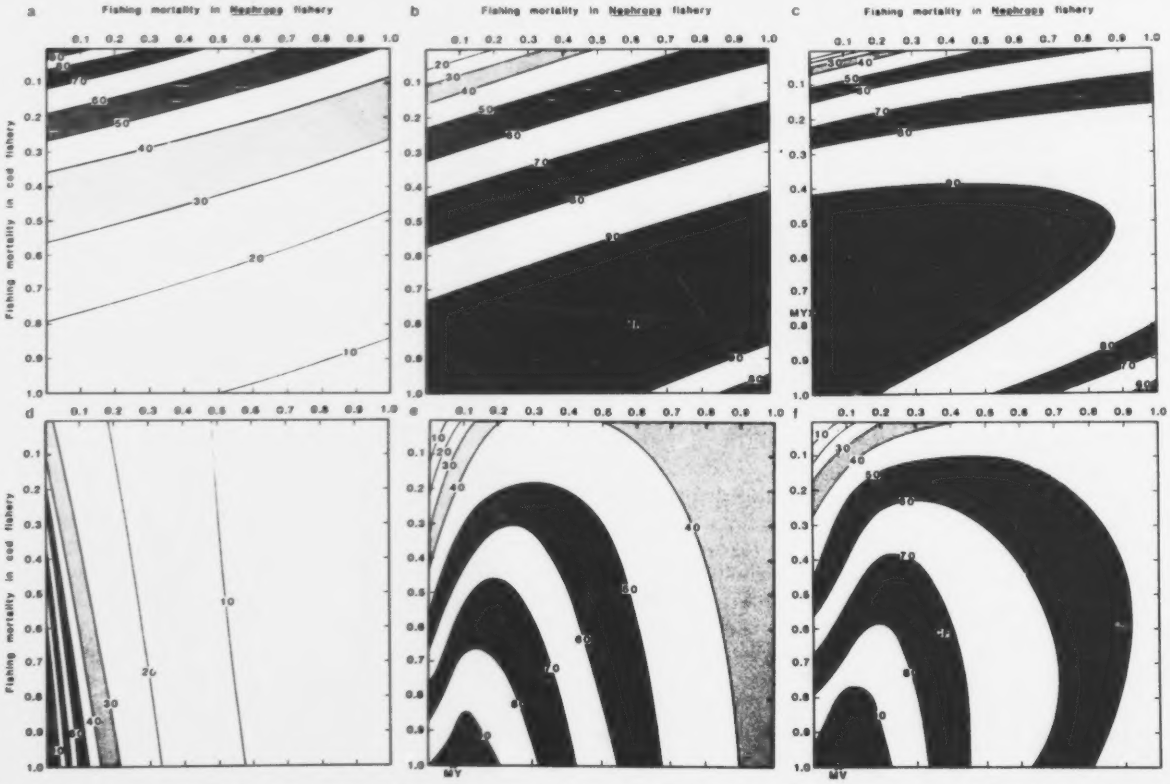

FIG. 11. Contour plots of the total fishery (Run 1). Contour lines are 10% intervals of the maximum. (a) Cod biomass: maximum is 54 K tonnes; (b) Cod recruitment: maximum (MR) is 7.7 million; (c) Cod yield: maximum (MY) is 8.7 K tonnes; (d) *Nephrops* biomass: maximum is 45 K tonnes; (e) *Nephrops* yield: maximum is 48 K tonnes; (f) Total value: Maximum (MV) = £12.4 million. CF = current fishing mortality in both fisheries.

TABLE 2. Comparison of output from the "standard run" at $F_{COD}=0.6$ and $F_{NEP}=0.3$ with independent estimates.

	Independent estimates	"Standard run"
COD		
Spawning stock biomass (t)	1173	1290
Recruitment (millions)	7.07	6.78
Yield (t)	8860	8290
NEPHROPS		
Spawning stock biomass (t)	9490	9670
Recruitment (millions)	(2000)	2000
Yield (t)	2753	2690
Weight of *Nephrops* eaten (t)	1033–1300	1544

estimates of these quantities. The match between them is very close and would be even closer if a second place of decimals was introduced in the F values and fractionally higher values were used. For example the weight of *Nephrops* eaten by cod is sensitive to small changes in F on *Nephrops*, dropping to 1191 t if F_{NEP} is increased to 0.4. However, given the uncertainty which surrounds the "independent estimate" of 1033–1300 t consumed, it would be unrealistic to make such fine adjustments at present.

We have shown that the model is capable of generating a set of values which are fully consistent with each other and with our best estimates of these quantities. We can now go on to look at the steady state consequences of applying different levels of fishing mortality. We can also look at the effect of varying the values of input parameters in order to determine which ones affect the outcome and which ones the model is insensitive to. Since some of these input parameters are poorly estimated, it will be particularly important to see what effect they have over a likely range of variability. If they have a big effect then more effort will have to be directed to improving the estimates, but if they have little effect then a rough estimate will do.

DESCRIPTION OF THE MAIN OUTPUT

To give an idea of the layout and quantity of output from the "standard run" the main results are contoured in Fig. 11a–e. Tables are also generated but not reproduced here. The F values in these Figures range from 0 to 1. There are two reasons for restricting the range of F values: (1) Our knowledge of the two stocks is obtained at levels of F close to the present values. The "domain of validity" of the model is therefore centered around the present levels and the results become increasingly uncertain as one moves away from them. (2) The range of F values used can be regarded as the "domain of feasible management" since it includes levels of fishing of between zero and two or three times the present values.

Table 3 is an extract from a much larger table. It shows the predation mortality generated by cod on each age group of *Nephrops* and the total weight of *Nephrops* eaten. The mortality rates are a function of cod biomass only, which depends in turn on the levels of F in the two fisheries. The weight eaten is a function of both cod and *Nephrops* biomass, which is why for example the weight eaten in line 3 ($F_{NEP}=0.3$, $F_{COD}=0.4$) is lower than in line 2, even though the mortality rates are higher.

The biomass of cod declines evenly as the level of fishing in the two fisheries increases (Fig. 11a). The cod stock will in fact collapse at F values slightly higher than the range shown here, but this is completely dependent on the choice of the recruit-per-biomass parameter (a) in the stock recruit relationship (S/R) which may not be well estimated. This aspect of the model's behaviour should not therefore be taken too seriously. In view of the uncertainty over the cod S/R relationship, this is one of the aspects whose sensitivity has been investigated and will be commented on later.

With the cod S/R relationship in the standard run, peak recruitment occurs over a fairly wide range of intermediate F values (Fig. 11b). Maximum yield (MY) occurs at $F_{NEP}=0$, $F_{COD}=0.76$ (Fig. 11c). This is also the maximum sustainable yield (MSY). The yield surface is fairly flat topped. In contrast to the picture of cod biomass, the *Nephrops* biomass has its highest value when F in the cod fishery is high (Fig. 11d). This is because cod biomass is then reduced, so that predation mortality is lower. *Nephrops* recruitment is not shown because the S/R relationship has been set to give a constant level at all values of *Nephrops* biomass (Fig. 7).

The highest *Nephrops* yield value occurs at $F_{NEP}=0.08$, $F_{COD}=1.0$ (Fig. 11e) with a small upper 10 percentile area. The highest value does not represent MSY, which lies outside the range of F values given here. In fact MSY occurs at $F_{NEP}=0$, $F_{COD}=1.6$, when the cod stock has collapsed and the large mesh (cod) fishery is being used to catch *Nephrops* only. This solution lies ouside the domain of validity of the model and will not be discussed further.

Figure 11f shows the monetary value of the two species added together and is probably the most useful presentation for considering joint management. The maximum value occurs at $F_{NEP}=0.07$, $F_{COD}=1.0$ and there is a fairly small upper 10 percentile area. The absolute maximum value coincides with MSY for *Nephrops* at $F_{NEP}=0.1$, $F_{COD}=1.6$. The contributions of cod and *Nephrops* to the maximum total value can be calculated easily from their yields and values; *Nephrops* contributes 75% of the total value and cod 25%.

This brief description of some of the seventeen tables and contour plots, which are routinely produced, gives some idea of the output, but also highlights the difficulty of presenting clear and concise results from different runs of the model. It is not easy to summarize or even to understand what is happening in a relatively simple two species, two fishery model such as this.

In the section on Results which follows we have adopted a visual presentation of the information on total monetary value from each run. Effectively this allows us to address the question "What will be the

TABLE 3. Predation mortality on *Nephrops* and total weight eaten by cod

Fishing mortality directed at		Predation mortality on *Nephrops* at age											Weight of *Nephrops* eaten (t)
Nephrops	Cod	0	1	2	3	4	5	6	7	8	9	10	
0.0	0.0	0	0	0.207	0.347	0.447	0.502	0.515	0.498	0.467	0.427	0.394	6535
0.2	0.6	0	0	0.177	0.182	0.168	0.147	0.125	0.103	0.087	0.072	0.062	2088
0.3	0.4	0	0	0.179	0.202	0.200	0.185	0.165	0.142	0.122	0.104	0.091	1817
0.3	0.6	0	0	0.174	0.177	0.162	0.141	0.119	0.098	0.082	0.068	0.059	1544
0.3	0.8	0	0	0.165	0.154	0.132	0.108	0.087	0.069	0.056	0.046	0.039	1309
0.4	0.6	0	0	0.171	0.172	0.156	0.135	0.113	0.093	0.078	0.064	0.055	1191
1.0	1.0	0	0	0.081	0.068	0.052	0.039	0.030	0.022	0.017	0.013	0.011	203

effect on the location of the maximum sustainable monetary value of altering this parameter?". In this way the sensitivity of the model can be tested in relation to one of the main concerns of strategic management. The maximum yields per recruit (MYR) and maximum yields (MY) have also been presented to allow comparison of management conclusions derived from the traditional single species assessment approach with the multispecies method presented here.

Results

THE "STANDARD RUN" (RUN 1)

Input and results from this run have already been described. Figure 11f shows the total value of the two species together; the highest value (MV) and the current fishing mortality (CF) have been marked on both. From this it can be seen that if the management strategy is to increase the total value of the fishery then fishing mortality should be reduced in the *Nephrops* fishery and increased in the cod fishery. On the other hand if the strategy is to increase the economic return, we can immediately say that the point of highest economic return must lie above and to the left of the point of highest value.

NO BIOLOGICAL INTERACTIONS (RUN 2)

One of the reasons given for choosing this model was that since it is an extension of existing yield per recruit models, as currently used in determining management strategy, a direct comparison can be made between the yield per recruit results and the interactive yield results. Run 2 of the model therefore uses the same input as the "standard run", except that the predation matrix is set to zero so that no predation occurs and M for *Nephrops* is set to 0.3 in order to compensate.

Figure 12 shows the MYR for cod and *Nephrops* if they were taken only in the respective directed fisheries. Apart from the use of a simpler exploitation pattern, which makes very little difference, the yield per recruit calculation for cod is exactly the same as that used by the International Working Group for this stock (Anon. 1983). The *Nephrops* stock is not assessed using yield per recruit methods at present.

The management strategy to obtain MYR on both stocks independently would be to aim for $F_{NEP}=0.25$, $F_{COD}=0.27$. We can now compare this with the interacting fisheries in the "standard run" (Run 1), the results of which are also shown on Fig. 12. The MSY for cod occurs at $F_{NEP}=0$, $F_{COD}=0.76$ and the highest sustainable yield for *Nephrops* within the domain occurs at $F_{NEP}=0.08$, $F_{COD}=1.0$. The upper 10 percentiles for both of these are shown and the MV point coincides with the *Nephrops* maximum.

The reason why the highest sustainable yield of *Nephrops* is in a different place from MYR is because of the effect of including the predation due to cod as a function of cod biomass. The reason why MSY for cod is in a different place from MYR is because of the stock recruit relationship used for cod. Since it can be argued that this relationship is not well determined, the effect of alternative shapes will be considered in the next section. For the present we can conclude that a model which includes the interactions between the two species may suggest a very different management strategy from single species yield per recruit models.

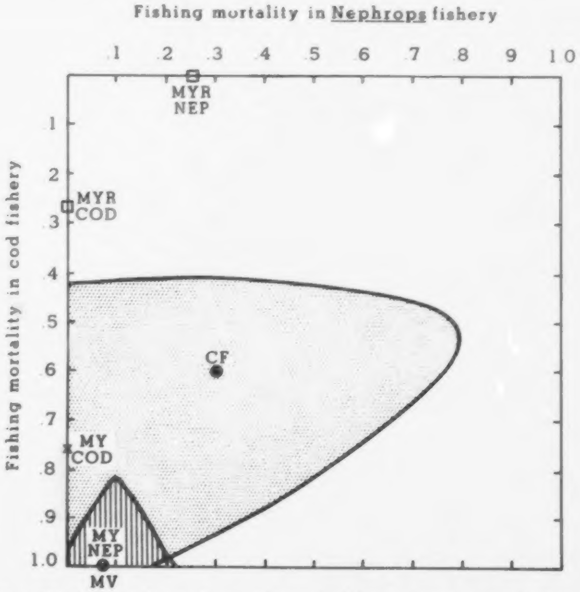

FIG. 12. Comparison of maximum yield per recruit (□MYR) in separate cod (COD) and *Nephrops* (NEP) fisheries with no predation, with maximum yields (x MY) and maximum value (○ MV) in the interacting fisheries. (CF = current fishing mortality in both fisheries (●); hatched areas represent 10 percentiles.)

ALTERING THE COD S/R RELATIONSHIP (RUNS 3 and 4)

The cod stock recruit relationship is not well determined and the shape of the curve will control the position of MSY. In order to look at the effect of different shapes, three different curves have been fitted (shown in Fig. 3) with β values of 1 (asymptotic), 2 (slightly domed) and 5 (highly domed). They all pass through the mean stock biomass, mean recruitment point and all have the same maximum recruit-per-unit-biomass (a) value.

The cod MSY points corresponding to these β values are shown in Fig. 13 with their upper 10 percentile areas. For $\beta=1$ the MSY lies below MYR, as it always must with a monotonically increasing curve, and the $\beta=2$ and $\beta=5$ points are much higher (for $\beta=5$ the MSY point lies just outside the domain). The choice of β value therefore is obviously very important in determining the management strategy for cod, but when the combined management of cod and *Nephrops* is considered, it appears that the choice of β has little effect. In fact the highest value (MV) for the two species is also shown in Fig. 13 and is the same for the three values of β. This result is partly due to the fact that the three different cod yield surfaces are fairly flat topped and partly due to the predominance of *Nephrops* in the total value.

The conclusion from this is that even if the actual relationship between cod stock and recruitment is less domed than in the "standard run", there is still a case for keeping fishing mortality on cod at or above the present level (CF).

Information on recruitment of *Nephrops* is not available and the MYR point, which assumes constant recruitment, therefore provides the only strategic guidance, if *Nephrops* were to be managed independently. Nevertheless, as with the cod, we can already say that MSY for *Nephrops* will only lie to the right of MYR if the stock recruit relationship is domed or if growth is density dependent.

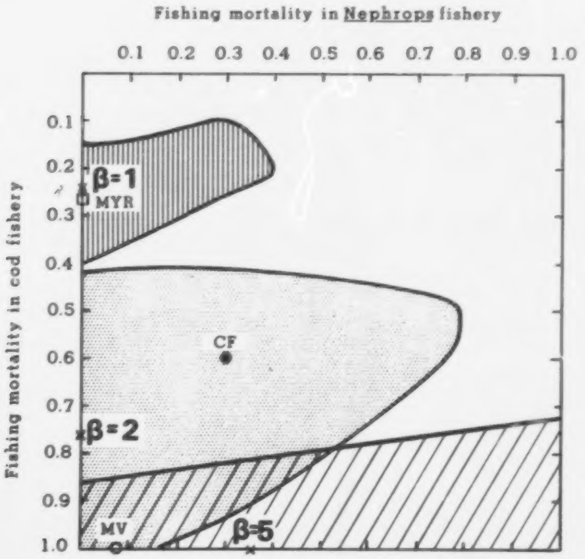

FIG. 13. The effect upon cod maximum yield (x, with hatched areas representing 10 percentiles) of changes in the β value of the cod stock–recruitment relationship. (CF = current fishing mortality in both species (●); MV = maximum value (O) of total fishery for all three β values; MYR = cod maximum yield per recruit (□)).

ALTERING THE FEEDING RELATIONSHIP (RUNS 5, 6, AND 7)

The section on "*Predation Mortality and the Functional Feeding Relationship*" gave the reasons for choosing the particular functional form of feeding relationship and parameter values. The question arises whether results of the model are affected critically by the function and parameter values used to describe feeding. If they are, then further work may be needed to improve our knowledge of feeding.

Three separate alterations were made to the input values used in the "standard run": (1) predation was allowed on all sizes of *Nephrops* and not just those over 0.6 g in weight. The effect of this is to generate predation mortality on 1-group *Nephrops* (Run 5), (2) the standard deviation of the size preference function was doubled to increase the mortality on a wider size range (Run 6), (3) the mortality per gram was increased by 50% to increase the predation mortality, but leave the distribution of mortality with size unchanged (Run 7).

The effect of these on the highest value (MV) is shown in Table 4 and as can be seen there is very little difference between them. The absolute level of yield may vary between the options, but the shape of the yield surface is hardly changed. Judging by this result it would appear that our existing knowledge of prey size preference is probably adequate. The level of predation mortality also does not seem to be very critical, but this conclusion will have to be reviewed when the estimate of *Nephrops* consumed by cod is improved.

THE EFFECT OF ALTERING THE MESH SIZE IN THE *NEPHROPS* FISHERY (RUNS 8 AND 9)

Results presented so far have tested the sensitivity and robustness of the model to changes in parameter values and functional forms. Next we look at an actual application of the model in order to evaluate the effect of a change in mesh size in the *Nephrops* fishery. The case for such an increase has been made for some time, based partly on the possible long term benefits to the

TABLE 4. The effect of various changes in the feeding relationship upon maximum value (MV £millions) and the corresponding cod and *Nephrops* fishing mortalities.

Run		MV	F_{COD}	F_{NEP}
1	"Standard run"	12.4	1.0	0.07
5	No truncation	11.5	1.0	0.07
6	2 × standard deviation	9.9	1.0	0.12
7	50% increase in mortality/g	10.0	1.0	0.09

Nephrops fishery, in improved yield per recruit, and partly on the beneficial effects for whiting and cod of a reduction in by-catch mortality in the small mesh fishery. Although cod has always been a less important component of the by-catch than whiting, it is worthwhile to use the model to examine the joint effects of possible mesh increases on cod and *Nephrops* together. It would be fairly straightforward to add whiting to the model at a later stage, if required.

The selection characteristics used in the "standard run" correspond to a mesh size of 55 mm and the effect of raising this to 60 mm and to 70 mm is examined in Runs 8 and 9. The input details were discussed in the section "*Nephrops Population Parameters*". In looking at the effect of a mesh change it is no longer sufficient to consider only the shape of the combined value surface, because changes in the absolute level are important. It may also be interesting to look at changes in the distribution of total value between the two species and between the two fisheries.

Table 5 shows that the highest value (MV) shifts very little due to these increases in mesh size, so that their effect on the strategy for fishing mortality in the two fisheries is very small indeed in absolute terms. There is quite a big relative effect however, because the MV with 70 mm mesh occurs at a fishing mortality in the *Nephrops* fishery which is 57% higher than when 55 mm mesh is being used. Table 5 compares yields and total values at the three different mesh sizes for the current level of fishing (CF) and for the level which gives the highest value (MV). The total value increases from £9.5M at CF with the current mesh size to £9.9M with a mesh size of 60 mm and £10.4M with a 70 mm mesh. This is due to increased yields of both cod and *Nephrops*.

The increase in total value by adjusting fishing mortality to MV is greater than the effect of the mesh change. The total value becomes £12.4M for 55 mm mesh, £12.5M for 60 mm and £12.7M for 70 mm. In fact if fishing mortality was adjusted to this level then mesh increase would make almost no difference.

Discussion

Three reasons were put forward in the Introduction to justify the modelling approach which we have followed and we can now go some way towards judging whether they were valid.

1) We have explored the effect of incorporating technical and biological interactions and S/R relations on the joint long term management strategy for the two species and results suggest that the present strategy based on single species yield per recruit analysis may be seriously misguided. This conclusion is robust under alternative input values for cod S/R relations, and under quantitative and qualitative changes to the FFR, which alters the predation mortality. The model therefore identifies serious doubts about existing management strategy and may already provide a more credible alternative.

2) Since our knowledge of the size preference aspect of the FFR is reasonably good and results are not sensitive to even quite big changes in the parameter values used, the work on this aspect of feeding need go no further. Other uncertainties in the relationship between total predator biomass and total prey consumed have been highlighted and probably justify further experimental and field work. The consumption rate of *Nephrops* by cod and the distribution of the cod stock into the proportion feeding and not feeding on *Nephrops* during the year both need to be re-examined. Nevertheless, in spite of the necessarily crude estimate of total consumption of *Nephrops* applied at present, the results are entirely consistent with independent estimates of mortality rate and *Nephrops* stock biomass. The model is already providing useful guidance on the kind of work which is needed to increase our confidence in the results shown here and in the consequent management strategy.

3) Within the "domain of validity" which we have set for the model the representation of the processes of growth, recruitment, feeding, and fishing seem appropriate. They differ from conventional yield per recruit analysis only in that they incorporate the additional information which we have on predation mortality and in that recruitment may be affected by parent stock biomass, which is essential for strategic modelling.

Results from this model could be misleading for three reasons. Our parameter values are poorly estimated, functional relationships are not appropriate, or because the model fails to incorporate some important aspect of the "real world" (such as another predatory link or the possibility that stochastic effects dominate the behaviour of the system in the long term).

Improvement in the estimation of rates and values used here is in progress, guided by our insight into their likely effect on the results. One particularly difficult parameter to estimate is natural mortality of *Nephrops* due to causes other than predation. This has been set at 0.1 in all runs which include predation mortality, but the reasoning behind this choice is not very logical. Morizur (1982) tabulated values of total mortality on nine "quasi-unexploited" stocks and these averaged 0.22 or 0.29 depending on the method used, but with the highest value at 0.41. This suggests that natural mortality, including predation would not be higher than

TABLE 5. Yields, fishing mortalities, and total values at different *Nephrops* mesh sizes. (CF = current fishing mortality $-F_{COD}=0.6$, $F_{NEP}=0.3$; MV = maximum value.)

	"Standard run"	Run 8	Run 9
Mesh size (mm)	55	60	70
Yield of cod at CF (K t)	8.3	8.4	8.6
Yield of cod at MV (K t)	8.1	8.1	8.2
F_{COD} at MV	1.0	1.0	1.0
Yield of *Nephrops* at CF (K t)	2.7	2.8	3.1
Yield of *Nephrops* at MV (K t)	4.0	4.0	4.1
F_{NEP} at MV	0.07	0.09	0.11
Total value at CF (£million)	9.5	9.9	10.4
Total value at MV (£million)	12.4	12.5	12.7

0.3. Our estimates of current fishing mortality, *Nephrops* biomass and *Nephrops* consumption by cod are in balance when the parameter values of the "standard run" are used and this gives a natural mortality on *Nephrops* of under 0.3, but with the predation component varying with age. Of course in our view the total mortality on a *Nephrops* stock will depend to a large extent on whether its predators are exploited and not only on whether the *Nephrops* are exploited, so that the table compiled by Morizur could be misleading.

Information on growth of *Nephrops* which we have used is rather limited, but further growth rate information will soon be available for the Irish Sea and a recent study (Bailey and Chapman, 1983) looks at growth rates in adjacent Scottish waters. Their rates for the Sound of Jura are similar to ones used here, but growth rates in the Clyde are higher and they suggest that this may be a density dependent effect brought about by different rates of fishing on the two populations. The effect of introducing density dependent growth into our model will be examined.

Because there are only two species in the model and cod suffers no predation or cannibalism, the biomass of cod is immediately determined without iteration and solutions are found quickly. Work by Armstrong (1982) suggested that poor cod (*Trisopterus minutus*) and pout whiting (*T. luscus*) were also significant predators on 0- and 1-group *Nephrops* in the Irish Sea and might in turn be eaten by cod. This would give rise to a more complex series of interactions, which would be difficult to treat quantitatively because of our ignorance of the respective biomasses, growth, mortality and predation rates. However more recent work (Symonds and Elson 1983; Patterson 1983) indicates that Armstrong's conclusions, which were based on sampling a limited area, are not representative and that poor cod and pout whiting are much less important than he supposed. There may however be other aspects of the "real world" which subsequently need to be incorporated in order to overcome exactly the kind of shortcoming which we think the existing yield per recruit models suffer from.

Management strategy for cod and *Nephrops* fisheries in the Irish Sea should be guided by results of this interactive model. This is not to say that the strategy should be entirely based on these results or should adopt the maximum value criterion as its main objective. What the model almost certainly does provide is a better long term forecast of the consequences of different regulations of fishing mortality and mesh size. However the model must be changed to take account of new information and changes in behaviour. For example the effect of an increase in mesh size on fishing behaviour of French vessels in the Celtic Sea in recent years has been examined and one cannot expect that the behaviour of the Irish Sea *Nephrops* fleet (i.e. the relative mortality which they generate on different species) would remain unchanged following a mesh increase. In any case, the long term benefit in total value of an increase in mesh size diminishes if fishing effort in the two fisheries moves towards MV, so that the case for a mesh change is linked to the changes in fishing mortality.

Conclusions

1) The relatively simple strategic model of the biological and technical interactions between cod and *Nephrops* in the Irish Sea gives a consistent and apparently sensible representation of their joint response to different levels of exploitation.

2) The model casts serious doubts about the use of single species yield per recruit analysis to guide the management strategy for the two species. It suggests that if the objective were to be to increase the joint value of the two species, then fishing mortality should be reduced on *Nephrops* but increased on cod.

3) The 2nd conclusion is shown to be fairly robust under variations in several of the parameters which are poorly known at present. If the model is to be used for detailed guidance on management strategy, then further sensitivity analyses on input values and assumptions will be needed.

4) By demonstrating which poorly estimated parameters are likely to influence the outcome of the modelling exercise, attention is focussed on areas which require further examination, notably the total consumption of *Nephrops*, the growth rate of *Nephrops*, and the mortality due to causes other than predation.

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Competition Among Lobsters and Crabs and its Possible Effects in Narragansett Bay, Rhode Island

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American lobsters (*Homarus americanus*), rock crabs (*Cancer irroratus*), and jonah crabs (*Cancer borealis*) are potential competitors in rocky subtidal areas of Narragansett Bay, Rhode Island. Here we review our efforts to determine the nature, mechanisms and results of this competition. Sampling by divers found lobsters and jonah crabs in rocky areas of Narragansett Bay while rock crabs were confined to sandy areas. In laboratory choice tests all three species selected rocky habitat when alone but rock crabs shifted to sand when a jonah crab was present. Shelters appeared to be a limited resource and in large laboratory tanks both species of crabs markedly decreased shelter use in the presence of lobsters, while lobsters decreased shelter use only slightly when competing with crabs. Jonah crabs were more likely to hold shelter than rock crabs in some tests but were equal in others. In aggressive encounters, lobsters always were victorious over both species of crabs, and jonah crabs defeated rock crabs. Relative body size had no effect on outcome of competition between lobsters and jonah crabs. All laboratory tests were conducted with a predator (*Tautoga onitis*) present. Under conditions of simulated competition for shelter lobsters suffered much higher injury and mortality rates than when competition was absent, while jonah crab mortality rates were unchanged. Jonah crabs are more flexible in their habitat use and loss of shelter though competition does not have as severe consequences as it does for lobsters. Interactions among the three species and fishermen were examined in a conceptual model and possible results discussed.

Le homard d'Amérique (*Homarus americanus*), le crabe commun (*Cancer irroratus*) et le crabe tourteau (*Cancer borealis*) peuvent se faire concurrence dans les zones rocheuses infratidales de la baie Narragansett (Rhode Island). Les auteurs résument leurs travaux visant à déterminer la nature, les mécanismes et les résultats d'une telle compétition. Un inventaire par plongeurs dans la baie Narragansett a permis de noter que les homards et les crabes tourteaux se trouvaient dans les zones rocheuses tandis que les crabes communs étaient confinés aux zones sableuses. Lors d'essais en laboratoire, les trois espèces ont choisi l'habitat rocheux quand elles se trouvaient seules, mais les crabes communs se déplaçaient vers les aires de sable en présence d'un crabe tourteau. L'abri s'est avéré être une ressource limitée et, dans les grandes cuves utilisées en laboratoire, les deux espèces de crabe délaissaient de façon marquée les abris en présence de homards tandis que ces derniers ne réduisaient que légèrement leur utilisation des abris quand ils étaient en compétition avec des crabes. Au cours de certains essais, les crabes tourteaux avaient plus tendance à conserver leur abri que les crabes communs, mais cette tendance n'a pas été notée au cours d'autres essais. Au moment des rencontres agressives, les deux espèces de crabes cédaient aux homards et les crabes communs cédaient aux crabes tourteaux. Le rapport des tailles n'avait aucun effet sur le résultat de la compétition entre les homards et les crabes tourteaux. Tous les essais de laboratoire ont été effectués en présence d'un prédateur (*Tautoga onitis*). Les homards présentaient des taux de blessures et de mortalité beaucoup plus élevés dans les conditions de compétition simulées pour les abris, tandis que les taux de mortalité des crabes tourteaux demeuraient inchangés. Ces derniers présentent une plus grande souplesse quant à l'utilisation et à la perte des abris de sorte que, comparativement au homard, les conséquences de la compétition sont moins sévères. Les auteurs traitent des interactions entre ces trois espèces et les pêcheurs, et de leurs résultats dans le cadre d'un modèle conceptuel.

Introduction

Three species of large decapods are found commonly in rocky and sandy subtidal areas of Narragansett Bay, Rhode Island: *Homarus americanus*, the American lobster; *Cancer irroratus*, the rock crab; and *C. borealis*, the jonah crab. Lobsters are found almost exclusively in rocky habitat (Cobb 1971; Cooper and Uzmann 1980.) Jonah crabs and, in many parts of their range outside Narragansett Bay, rock crabs are also found in rocky areas (Scaratt and Lowe 1972; Haefner and Teretta 1971; Haefner 1976, 1977.) The three species seem to have similar habitat requirements, and additionally feed on similar prey (Weiss 1970; Scarrat and Lowe 1972; Jones 1973.) They probably also share similar predators (Reilly and Saila 1978; Cooper and Uzmann 1980.) They do not, however, share similar fishing pressure. The fishery for *H. americanus* is one of the largest and most valuable on the east coast of the USA. Eighty to ninety percent of legal sized lobsters are removed from the inshore stock annually. There is a small market for jonah crabs which are taken largely as a by-catch of the lobster fishery. Rock crabs are a by-catch of trapping and trawling but have no significant market.

In any group of species that share common resources, there is the possibility of competitive interrelationships. Jeffries (1966) showed that in Narragansett Bay *C. irroratus* is found in sandy areas and suggested that interactions with *C. borealis* may exclude it from preferred rocky areas. An inverse relationship between number of lobsters and number of crabs caught in lobster traps has been documented (Stasko 1976; Krouse 1978; Fogarty and Borden 1980) and could reflect actual abundances in study areas or it could be the result of interaction in the trap (Richards et al. 1983.) If competition and/or predation occurs among these three species it would have very different implications to the fishery than if the species act independently.

Results we present here show that competition is an important factor affecting distribution and mortality of the three species. The paper is in three parts. First, we review our observations on the small-scale distribution in Narragansett Bay and the habitat-related behavior of the three species. Second, we present results of field and laboratory experiments on the nature and mechanisms of competition among the species and evidence that in the presence of competition, mortality rates change in unexpected ways. Finally, in the Perspectives section, we consider the implications of these interspecific interactions to the lobster fishery, and vice versa. Because this is an overview, emphasis on methods will be slight. Original data and methods are found in several theses (Fogarty 1976; Richards 1981, 1984; Wang 1982) as well as in a series of papers submitted or in preparation.

Microdistribution and Habitat Behavior

1. Habitat Use and Habitat Selection of Crabs and Lobsters in Narragansett Bay

In field sampling by Fogarty (1976) five m^2 quadrats were randomly placed in each of four substrate types (rock, sand, mud, and gravel) at depths from 1.75 to 10.25 m. *Homarus americanus* was found only on rocky substrates and *C. irroratus* occurred in sandy areas only. *Cancer borealis* occurred on a slightly wider array of substrate, occupying rock habitats extensively and gravel and mud to a lesser degree (Table 1). A few *C. borealis* were found on mud, but so few that it is omitted from the table.

TABLE 1. Density estimates (# per m^2) for lobsters, jonah crabs, and rock crabs in Narragansett Bay R.I., based on 50 randomly placed 5 m^2 quadrats in each substrate type. Standard deviation is given in parentheses.

	Rock	Sand	Gravel
H. americanus	0.35 (0.28)	0.00	0.00
C. borealis	0.48 (0.41)	0.00	0.03 (0.08)
C. irroratus	0.00	0.42 (0.26)	0.00

Both *H. americanus* and *C. borealis* excavate burrows beneath rocks and boulders. In rocky areas, the shelter appears to be a discrete resource unit. Of 177 shelters examined by Fogarty (1976), 88% were occupied singly. The remaining 12% were occupied by two or more individuals of *C. borealis* (9%) or by a *C. borealis* – *H. americanus* pair (3%). No instances of two *H. americanus* in the same shelter were seen. There did not appear to be major differences in the shape of the shelters used by the two species (Richards 1984) although lobsters often have shelters with two or more openings (Cobb 1971) while crab shelters usually have only one entrance (Wang 1982).

Laboratory studies of habitat selection by the two species of *Cancer* were conducted in aquaria in which the bottom was divided into quarters each covered with one of four substrate types: sand, mud, coarse gravel, and rock. Rock substrate was arranged so a crevice was available for shelter: the other three substrates were deep enough so the animals could bury completely. One hundred fifty individuals of each species were tested singly, subsequently 100 trials with a *C. borealis* - *C. irroratus* pair were run. *Cancer borealis* when alone occupied the rock sector in 80% of the trials, the sand sector in 11% and mud and gravel to a smaller extent (Fig. 1A.) Similarly, when alone *C. irroratus* chose the rock area in 62% of the trials and the sand in 23% with

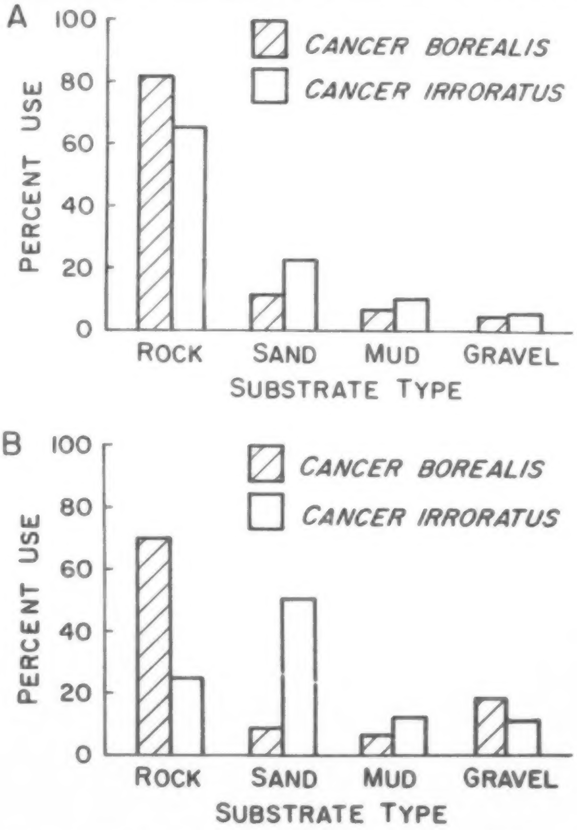

FIG. 1. Substrate choice in the laboratory by individuals of *Cancer borealis* and *C. irroratus* when alone (top graph, $N = 150$) and by *C. irroratus* and *C. borealis* when an individual of the other species was present (bottom graph, $N = 100$.)

mud and gravel less frequently occupied. The relative proportion with which each substrate was used by *C. irroratus* changed significantly ($\chi^2 = 36.8$, $P<0.05$) in the presence of *C. borealis*. Resource use by *C. borealis* also was affected by the presence of *C. irroratus* ($\chi^2 = 20.3$, $P<0.05$; Fig. 1B).

2. BURROWING AND BURYING BEHAVIOR

Cobb (1971) described how lobsters excavate shelters and Fogarty (1976) how *C. borealis* and *C. irroratus* bury themselves in sand. Burrowing and burying are fundamentally different behaviors. The first is used to construct a cavity or depression, the second to submerge the animal in the sediment. Lobsters do not bury and crabs, particularly *C. irroratus*, seldom burrow. For this reason lobsters are much more strongly adapted (and tied) to shelter use than are the two species of *Cancer*. When buried, *C. irroratus* is usually almost invisible except for the eyestalks and second antennae, while *C. borealis* seldom buries deep enough to cover the entire carapace. Mean time to complete burying differs significantly (ANOV, $F=390.3$, $P<0.05$) between the two species (*C. irroratus*: 16.3 seconds, *C. borealis*: 48.9 seconds). *Cancer borealis* excavates shelters to some extent, using the chelae to push sand or mud out of the shelter. Thus of the three species, lobsters seem to be best adapted to exploit the rock/shelter environment, and *C. irroratus* best adapted for the sand environment, with *C. borealis* more of a generalist able to use both.

3. ACTIVITY RHYTHMS

Lobsters are nocturnal animals (Weiss 1970; Cooper and Uzmann 1980), generally emerging from shelter just after sunset and returning before sunrise. Fogarty (1976) observed activity rhythms of individual *C. borealis* and *C. irroratus* in the laboratory under a 14:10 light: dark cycle to simulate summer conditions. Both crab species clearly are nocturnal but differences in the proportion of day and night activity are apparent (Fig. 2A.) These results can be compared with activity rhythms of lobsters studied in the same tanks 7 yr earlier (Fig. 2B, from Cobb 1969.) In all three species there is a marked increase in activity after the beginning of the dark phase but *C. irroratus* exhibited lower nighttime and higher daytime activity than did the other two species. Field observations corroborate this; actively foraging *C. irroratus* were noted during daylight hours, but *C. borealis* and *H. americanus* are rarely seen out of shelter during the day (Fogarty 1976.) In large naturalistic tanks (4-m diameter pools supplied with sand and shelter) with both crabs and lobsters present, both species of *Cancer* generally emerged from their shelters later than lobsters. Lobsters returned to shelter frequently during the night, but crabs took shelter or buried only at dawn (Wang 1982).

Competition: Mechanisms and Effects on Mortality

Our observations on lobster behavior and Fogarty's (1976) habitat selection experiments on crabs (described above) implied that competition exists among the three species. However, confirmation only came through further field and laboratory manipulations. It should be noted here that field removal experiments reported below involved sublegal size lobsters almost exclusively since intense fishing pressure selectively removes almost all the legal-sized (>81 mm carapace length) (CL) lobsters. Laboratory experiments, designed to follow up field work, similarly were done with sublegal lobsters and a wide size range of crabs. If competition has been a factor in structuring the decapod assemblage, then presumably removal by the fishery of nearly all the larger lobsters would change the course of the competition. To understand past effects of competition, experiments should be run on unfished populations with pre-fishery size structure. Unfortunately such populations are not available.

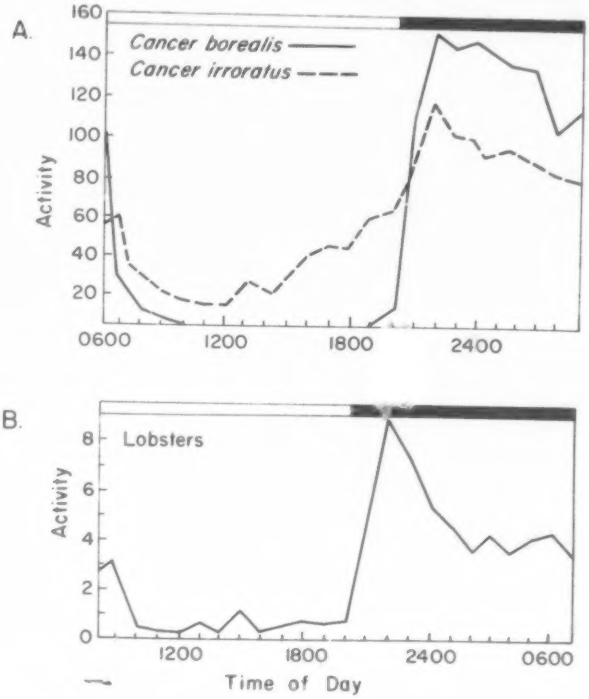

FIG. 2. Diel activity patterns of two species of *Cancer* (top graph) and of *Homarus americanus* (bottom graph). For *Cancer* the data were summed over days and individuals for a 5-d period. The lobster data are mean activity for eight animals over a 7-d period. Observations were made in the same activity chambers at approximately the same time of year.

1. DOES COMPETITION EXIST AMONG THE THREE SPECIES?

A. Field Experiments

Field manipulations consisted of removing lobsters from test areas and comparing crab population densities in treatments with both temporal and spatial controls. Four quadrats, 3 m × 10 m, in a rock–sand substrate were established. *Cancer borealis* and *H. americanus* were the dominant species in the area:

C. irroratus was not present. All four quadrats were censused initially (pretreatment temporal control) then lobsters were removed from two of the quadrats approximately every other day for 3 wk (test 1) then all lobsters were removed from the same two quadrats every day for a week (test 2), finally all four quadrats were censused again two weeks after treatment ceased (post treatment control). The two quadrats that were not subjected to treatment were censused during the treatment periods, thus acting as spatial controls.

Lobster removal did not always alter lobster density. In test 1, removal of lobsters approximately every second day had no effect on the size of the lobster population when compared to control quadrats. However when lobsters were removed daily (test 2) average daily density of lobsters was 0.19/m^2; in control quadrats during test 2 it was 0.50/m^2, a significant difference (Wilcoxon Signed Rank Test, $P=0.006$). Despite intense efforts at removal, lobsters were always present in the area, indicating significant immigration to quadrats on a daily basis. All removals were made during the two hours after dusk when the animals are most active. Thus we suspect the treatment reduced habitat use by lobsters as well as lowering density, even though we could not remove all the lobsters.

The lobster removal treatment resulted in an increase in density of *C. borealis* during test 2, but not during test 1 (Fig. 3.) Increase in crab density was largely accounted for by an increase in number of small crabs (<50 mm carapace width (CW) (Table 2).

B. *Competitive Behavior in the Laboratory*

Quantitative and qualitative observations of competitive behavior among *C. borealis, C. irroratus* and *H. americanus* were made by Wang (1982) in large naturalistic tanks. The tanks (4 m diameter × 1 m deep circular swimming pools) were supplied with sand bottom, 5 appropriately sized shelters and a predatory fish (a single tautog, *Tautoga onitis* 42–45 cm fork length.) The number of shelters was always less than the number of animals, so competition for shelter would be a possibility. The tautog was used because it quickly became clear in preliminary experiments that unless a predator was present, shelter use by crabs was lower than expected from field observations. The fish was an effective predator; attacks on crabs and lobsters were seen and occasional mortality occurred.

One of the questions asked was how the presence and density of a competitor affects the use of shelter by either species of crab or by lobsters. To answer the question, 5 members of the test species were put in the tank with 0, 3, 5, or 10 members of a second species. When three of the second species were in the tank the density of animals was approximately equal to natural densities observed in the field, which range from 0.2 to 0.5 per m^2 for all three species in suitable habitat. Size was not a treatment variable in these experiments. Lobsters used ranged from 41 to 81 mm CL and crabs from 41 to 121 mm CW. In any given replicate lobster size was within a 20 mm range, while crab sizes varied according to availability. Average crab size did not vary more than 9% among treatments. Shelter use by lobsters was not affected by density of either species of crab (*C. borealis* $\chi^2=3.6$, $P>0.05$; *C. irroratus* $\chi^2=2.5$, $P>0.05$) although shelter use declined from 100% to 80–90% in the presence of crabs, without regard to species or density (Fig. 4). The rock crab, *C. irroratus*, showed no change in shelter use in the presence of the jonah crab ($\chi^2=2.93$, $P>0.05$) but showed a marked decrease in the presence of lobsters ($\chi^2=11.9$, $P<0.05$). The proportion of *C. borealis* using shelters was not affected by the presence or density of *C. irroratus* ($\chi^2=0$). However the presence of lobsters significantly decreased ($\chi^2=19.4$, $P<0.05$) shelter use of jonah crabs from 80% under no competition to 40–50% at intermediate densities and to 0% at the highest densities of lobsters. Of the three species, *H. americanus* was the most likely to occupy shelters singly and *C. irroratus* the least (Table 3.)

There were a number of interspecific agonistic encounters in which a clear winner and loser could be distinguished. Of the encounters beween lobsters and *C. irroratus*, lobsters won 86%. Lobsters won 50% of their encounters with *C. borealis*. Encounters between *C. borealis* and *C. irrorratus* were infrequent, but *C. borealis* won all of them.

Taken together, these results indicate that *H. americanus* is the best competitor for shelter, with *C. borealis* second and *C. irroratus* third. Thus the answer to the question asked at the beginning of this section, "does competition exist among these three species?" seems to be yes. When shelters are limited, competition exists, and is mediated by aggressive interactions. We next explored how relative body size and predator pressure could modify the nature of competition between *H. americanus* and *C. borealis*.

2. COMPETITION AND RELATIVE BODY SIZE

Relative size of combatants in any interaction among crustaceans generally has an important effect on the outcome of an encounter. Briefly, the larger animal usually wins (Hyatt 1983.) We assumed that this would be true as well for interspecific competition among

TABLE 2. Mean daily densities (#/m^2) of crabs and lobsters in both control quadrats over all periods and test 2 (intense lobster removal) quadrats in Narragansett Bay. Small crabs were <50 mm CW, small lobsters were <40 mm CL. Standard deviation is given in parentheses. Distributions of crab densities in controls and test 2 are different (Wilcoxon Rank Sum Test: for all crabs $P=0.054$; for small crabs $P=0.0004$).

Cancer borealis	All crabs	Small crabs
All Controls	0.20	0.07
	(0.14)	(0.09)
Test 2	0.30	0.21
	(0.18)	(0.14)
H. americanus	All lobsters	Small lobsters
All controls	0.33	0.19
	(0.15)	(0.10)
Test 2	0.19	0.14
	(0.05)	(0.04)

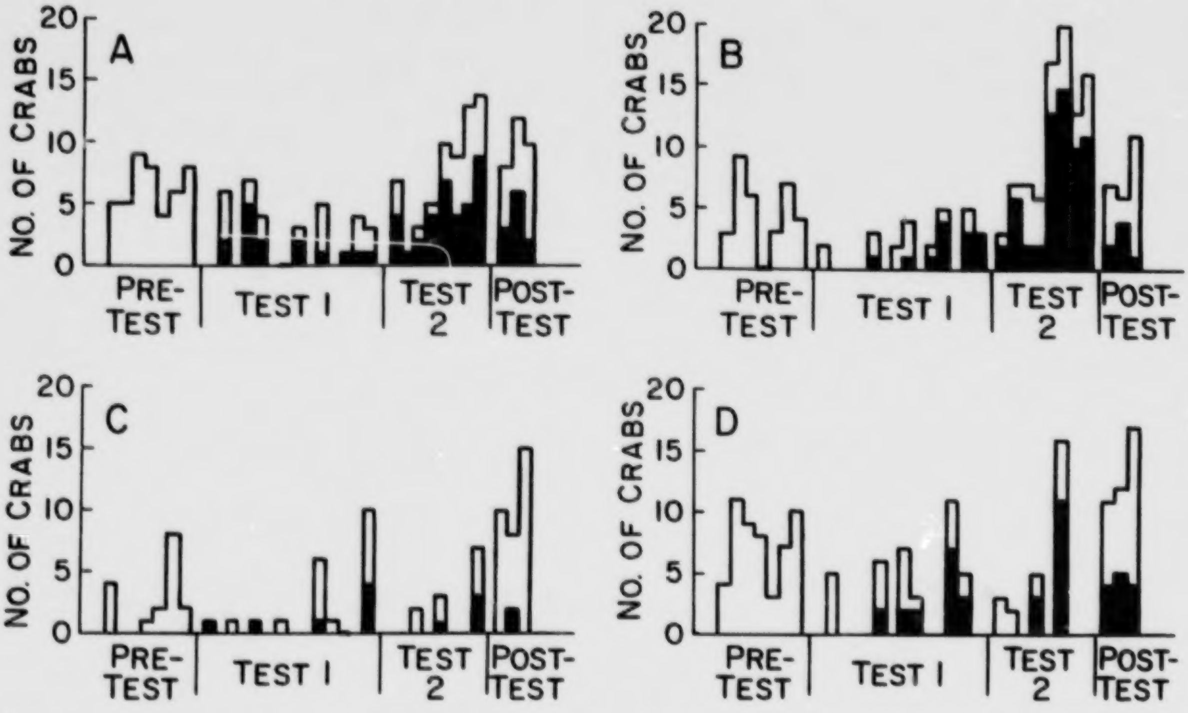

FIG. 3. The numbers of *Cancer borealis* seen on each dive in the lobster removal quadrats and the control quadrats for the pretest, two test and the posttest periods. The crabs were divided into two size classes after the pretest period; small (<50 mm CW, shaded) and large (>50 mm CW, open).

TABLE 3. The frequency of multiple shelter occupation in large naturalistic tanks in competition experiments between pairs of species.

	Alone	With another individual	Not in shelter	# Occupied shelters
H. americanus	83.3	13.9	2.8	72
C. irroratus	1.4	12.5	87.9	
H. americanus	48.8	38.1	13.1	84
C. borealis	2.4	42.8	54.8	
C. borealis	28.3	36.7	35.0	60
C. irroratus	18.3	41.7	40.0	

crabs and lobsters and set out to determine the "break point" in relative body size between *H. americanus* and *C. borealis* where the competitive advantage tipped from one to the other. We assumed that at some point large *C. borealis* would be able to dominate smaller *H. americanus* and thus control the shelter resource.

The effect of size differences between crabs and lobsters was tested under conditions of competition and no competition (Richards 1984.) Medium (49–59 mm CL) sized lobsters were tested against small (65–91 mm CW), medium (98–124 mm CW) and large (132–158 mm CW) *C. borealis*. As before, the predator *T. onitis* was present in the tanks for all the tests, but this time two fish were used in each experiment. The fish used ranged from 34 to 52 cm total length. With few exceptions, these experiments showed no effect of animal size on the outcome of competition for shelter. There was no effect of crab size on shelter use by lobsters. Under conditions of competition, medium sized crabs decreased shelter occupancy relative to the other two crab sizes. Mortality rates were significantly greater (Wilcoxon Rank Sum Test, $P<0.05$) for lobsters than for crabs in treatments with competition but there was no significant difference between lobster and crab mortality in the controls (Wilcoxon Rank Sum Test, $P>0.05$). There was no effect of crab size on crab mortality, nor was there a difference in crab mortality between experimentals and controls (Wilcoxon Rank Sum Tests, $P>0.05$).

These results are counter-intuitive. One would expect that larger crabs would be more successful in aggressive interactions over shelter than smaller crabs, and that lobsters, with larger claws and a more active escape response, would suffer less mortality than crabs. The issue of differential mortality rates will be addressed in more detail in the next section. Perhaps part of the explanation for the lack of size effects lies in the nature of the competition. Before these experiments we had emphasized the importance of aggression. However, other factors also are important. According to Wang's (1982) observations crabs leave their shelters later in the evening than lobsters and return only at dawn, while lobsters return frequently to shelter during the night. The advantage of prior residence in an shelter may outweigh any size advantage. In this way lobsters may use the shelter resource more effectively than crabs and

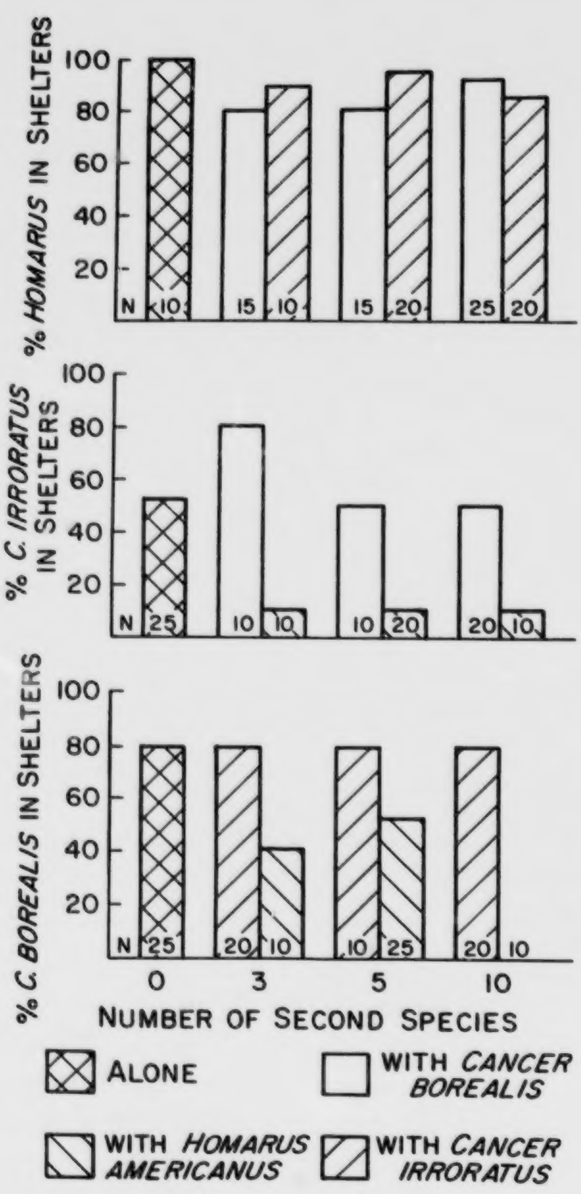

FIG. 4. Average numbers of *Homarus americanus* (top), *Cancer irroratus* (middle), and *C. borealis* (bottom) in shelters when alone or in the presence of different numbers of animals of each of the other two species. Each replicate used five test animals; the total number of animals observed is given inside each histogram.

gain an advantage in what has been called pre-emptive competition (Schoener 1983). The tactics of shelter defense by *C. borealis* also may help obviate the effects of size. When threatened in shelter, *C. borealis* jams itself in as tightly as possible, folding its claws and legs and becomes motionless. In effect it "pretends it is a rock" and changes the dimensions of the shelter, making it less suitable for a competitor trying to enter. This too could be classified as a type of pre-emptive competition.

3. HABITAT SELECTION, COMPETITION, AND MORTALITY

Further habitat selection studies were conducted in the large naturalistic tanks using only *H. americanus* and *C. borealis* in order to refine our understanding of the nature and effects of competition between the two species. In these experiments (Richards 1984) the bottom of the tanks were divided into three equal pie-shaped sections; one with cobble substrate, the second with sand, the third with sand plus shelter. Two predatory fish (*T. onitis*) were included. Since earlier work indicated shelter appeared to be a limiting resource the habitat selection experiments were run twice, once with twice as many shelters as animals in the "sand with shelter" section (control, no competition) and once with half as many shelters as animals (experimental, competition.) Five crabs and five lobsters were used in each test. At least 45 replicates were performed for each treatment. The resulting data are summarized in Table 4.

As in earlier experiments competition significantly reduced the proportion of animals using shelter and increased shelter sharing. *Cancer borealis* decreased shelter use more than lobsters and the use of cobble and sand substrates by crabs increased significantly. In contrast lobsters unable to obtain shelter excavated burrows underneath the shelters. Mortality due to the actions of the two predatory fish increased markedly for lobsters but not for crabs. The average mortality rate for crabs was the same, 0.03, in control and experimental treatments, while for lobsters it increased from 0.02 in the controls to 0.11 in the experiments. Other prey choice experiments showed the tautog consumed lobsters and crabs in equal proportions when presented in equal numbers in featureless tanks.

To further examine the differences between crab and lobster mortality, habitat specific mortality rates were determined in large naturalistic tanks. The experiments

TABLE 4. Proportion of animals in each sector of a large tank with three equal size areas of cobble, sand and sand with shelter substrates. The habitat selection tests were run twice (30 replicates each) once without competition (twice as many shelters as animals) and once with competition (one-half as many shelters as animals). All lobsters were in the medium size range (49–59 mm CL), the crabs were of 3 sizes: Small (S) = 65–91 mm CW; Medium (M) = 98–124 mm; Large (L) - 132–158 mm. EXP = Experimental treatment, CONT = Control treatment.

Crab	Cobble		Sand with Shelter		Sand	
size	EXP	CONT	EXP	CONT	EXP	CONT
			Cancer borealis			
S	0.49	0.32	0.36	0.67	0.07	0.02
M	0.40	0.15	0.49	0.82	0.09	0.02
L	0.09	0.03	0.57	0.85	0.31	0.03
			Homarus americanus			
S	0.00	0.00	0.90	0.99	0.00	0.00
M	0.01	0.00	0.85	1.00	0.00	0.00
L	0.01	0.00	0.78	0.93	0.00	0.00

were similar to the habitat selection experiments except that the pool contained only one substrate for each test: either cobble, sand, or sand with shelters. Five individuals of *C. borealis* and 5 of *H. americanus* were placed in the tank 1 h before introduction of the predators. Twenty replicates were performed for each substrate type. Lobster mortality and injury rates were significantly higher in the cobble and sand habitats than in the shelter habitat. Crab mortality and injury did not change significantly with habitat type (Table 5.)

The great difference in lobster and crab mortality rates was unexpected. Clearly the loss of a shelter or the failure to win in competition has much more severe consequences for a lobster than for a Jonah crab. In the cobble habitat treatment of the habitat specific mortality experiments for instance, 50% of the lobsters were killed or injured while only 3% of the crabs were. By contrast, the injury plus mortality rates for lobsters and crabs were 5 and 11%, respectively, in the sand with shelter habitat. Crabs can bury themselves in both sand and cobble as well as use shelter and thus are more flexible in their use of habitat than are lobsters. Before completing these experiments it seemed to us that by being the superior competitor for burrows lobsters would significantly increase their fitness relative to crabs. However, this conclusion no longer is as clear due to the difference in mortality rates.

TABLE 5. Number of *H. americanus* and *C. borealis* killed and injured in three different habitat types in laboratory experiments. The number of animals tested was 100 in each case. Asterisks indicate significant differences in mortality or injury between cobble or sand and sand with shelters (χ^2 tests, * = $P<0.01$)

	Cobble	Sand	Sand with Shelter
Losters			
Mortality	31*	25*	2
Injury	19*	15*	3
Crabs			
Mortality	2	7	6
Injury	1	7	5

Perspectives on Ecological Competition and the Lobster Fishery

We have shown that in Narragansett Bay competition is one factor structuring the assemblage of larger benthic decapods in rocky subtidal habitats. Lobsters outcompeted *Cancer* crabs for burrows and *Cancer borealis* appeared to be a better competitor than *C. irroratus*. All three species decreased burrow use in the presence of a competitor. In some cases the density of competitors relative to the density of useable shelters as well as preemptive competition affected shelter use. In our experiments the relative size of the competitors did not affect the outcome. Mortality of lobsters without shelter increased markedly while mortality of *C. borealis* under similar conditions did not. Behavioral aggression between species may be important in determining presence or absence in a microhabitat, but first use may be more important for the monopolization of an individual shelter.

Our goals in the field and laboratory experiments and in conceptualizing the system were first to develop information and formalize our knowledge of the interactions and second to try and understand the effects of the interaction between ecological competition and fishing pressure. The perturbation experiments we performed in the field and the laboratory experiments done in large tanks were an attempt to evaluate the direct effects of one species on the other. Clearly these experiments were not complete. Because of the complex nature of marine ecosystems and the enormous effort needed to do the appropriate experiments and observe all the species, from parasites to predators, that might affect the results indirectly (see Bender et al. 1984 for a discussion) it is nearly impossible to have complete confidence in predictions made from the results of the experiments. As Bender et al. say, this is a sobering thought. Thus despite a considerable amount of laboratory and field experimentation, unknown factors, especially indirect ones, may be affecting our results. The laboratory experiments and short term field experiments we performed are not the same as the long term removal experiments needed to predict with real confidence the effects of one species on the others. Capelli and Munjal (1982), taking crayfish as an example, have cautioned about extrapolating from behavioral results in the laboratory to the outcome of competition in the field. However, our results from field and laboratory reinforce one another and we assume they represent the basic nature of the interactions. From these results we wish to speculate a bit about what the long term effects of the lobster fishery have been and what might happen if a greater fishing pressure were to be imposed on the crabs. It should be remembered that our experiments involved sublegal size lobsters almost exclusively. Thus our results are most appropriately applied to the situation as it currently exists with regard to lobster and crab population densities and size structures.

To put some format to our speculation about ecological competition and the fishery we attempted to use loop analysis (Levins 1975) but found that despite (or perhaps because of) the simple nature of the system the results were less than satisfactory to us.[1] Nevertheless we found the general type of structural diagram used in loop analysis and food web diagrams (e.g. Paine 1980) to be useful for speculating about how the system might respond to changes. The reasoning we use is similar to that of Caddy (1983) in his musings on the effect of single-and multispecies harvesting of trophically linked species. Figure 5 shows our concept of how the simple lobster – crab – predator – fishermen system is structured. Lobsters compete with jonah crabs and are preyed upon by fishermen and unspecified predators. Lobsters are separated into legal (>81 mm CL) and sublegal sizes because the standing stock of legal lobsters is clearly very small: for example in Wang's (1982) removal experiments none of the 108 captured lobsters were of legal size. This does not necessarily imply that the production of legal sized lobsters in Narragansett Bay is small, only that the turnover is high due to the intense fishing pressure. Because the standing stock of large lobsters is small their interrelationships with other species are considered slight and are not included in the diagram.

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[1] For those readers interested in our loop analysis and critique thereof, an addendum is available from the first author.

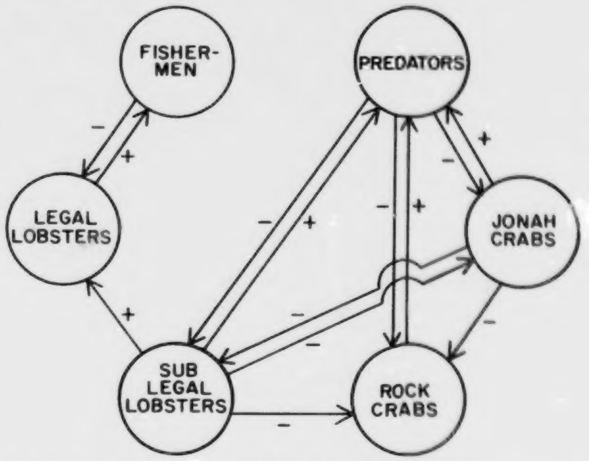

FIG. 5. Structural diagram of the lobster–crab system. Arrows show interactions; a + sign associated with the arrow indicates a positive effect on the element at the receiving end of the arrow, a − sign the opposite. See text for discussion.

Rock crabs are part of the system only through two links indicating the negative effects lobsters and jonah crabs have on them. In fact, rock crabs generally are not found in the rocky subtidal of Narragansett Bay and we postulate this competition explains their absence from an apparently preferred habitat. Thus, if lobster and jonah crab populations were to decrease there probably would be an increase in rock crabs.

Fishermen clearly have decreased the size of the population of legal sized (>81 mm CL) lobsters. We suspect this has released some of the competition with jonah crabs, allowing their population to increase. It may also have resulted in an increase of juvenile (sublegal, <81 mm CL) lobster survival due to release of intraspecific competition. Because jonah crabs and sublegal lobsters compete for similar sized shelters the increase in the jonah crab population would probably cause a higher mortality of lobsters due to predation. Thus the effect of fishing on the lobster population may be twofold: first a reduction of large lobsters, directly attributable to fishing, and second a loss in the potential size of the population of smaller lobsters due to the increase in competition from jonah crabs, indirectly attributable to the fishery.

It is fruitless to speculate what might happen should there be a decrease in fishing pressure on lobsters: it is most unlikely to occur. It is more likely that a larger market for jonah crabs might be developed. An increase in fishing for jonah crabs clearly would reduce their population size. What else might happen? Fewer jonah crabs would mean less competition with sublegal lobsters, providing lobsters with more shelters and a lower loss to predation. Thus, presumably there would be a greater recruitment to the fishable stock of lobsters. Rock crabs probably would be unaffected since the increased population of small lobsters would continue a high level of competitive pressure. Thus a multispecies fishery (or two directed fisheries) might have the effect of increasing the lobster catch as well as exploiting a resource (jonah crabs) that currently is little used. There seems to be a good argument for lobstermen to encourage the development of a market for jonah crabs.

It would be a mistake to view man simply as a predator in this (or any harvest) system. As Hennemuth (1979), among others, has pointed out, human intervention is an external perturbating force. Fishing pressure, unlike predator pressure, is regulated by market forces as well as availability of prey. In the case of lobsters at least, market forces are largely outside the system so feedback to the ecosystem in the form of effort restriction is slight.

The study of both ecological competition and of fisheries biology are long established endeavors. Nevertheless the attempt to combine interspecific interactions and human exploitation is relatively recent and with few exceptions (e.g. Silliman 1975; Momot and Gowing 1977) limited to analysis by use of models. The present study is no different: confident statements about the effect of fishing pressure on the populations of lobsters and crabs must await the next logical experimental step: manipulation of fishing pressure.

Acknowledgments

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Review of the Biology and Fishery Status of Cephalopods in the Gulf of Thailand

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Cephalopods caught in Gulf of Thailand fisheries consist of octopus, squid, cuttlefish, and chambered nautilus and include 8 families, 14 genera, and 24 species. Commercially important squid and cuttlefish include: *Loligo formosana, L. duvaucelii, Sepioteutis lessoniana, L. tagoi*, and *Sepia aculeata, S. pharaonis, S. lycidas, S. recurvirostra, S. brevimana*, and *Sepiella inermis*, respectively. Length–weight relationships, sex ratios, size at maturity, fecundity, and food contents of some species were studied during the past few years. The catch of cephalopods increased steadily from 11 602 t in 1965 to a peak of 93 694 t in 1977, since then production has fluctuated.

Squid and cuttlefish are caught mostly by bottom trawls in offshore waters and by push nets and lift nets in inshore and coastal waters. Both otter trawls and pair trawls are used in the offshore fishery. The most productive fishing grounds for squid and cuttlefish are in the northwestern part of the Gulf of Thailand where the average water depth is 25 m.

A preliminary estimate of maximum sustained yield of squid stocks exploited by trawl fisheries was about 42 000 t. However, the potential harvest of the entire stock, which includes non-trawlable stocks or pelagic forms, in the entire Gulf of Thailand is not known. Potential yields for cuttlefish and octopus are not known.

Biological information on each species group is insufficient for stock assessment purposes. Major areas for future research are proposed.

Necessary studies for rational fisheries management which includes regulation of traditional fisheries, introduction of non-traditional fishing methods and mariculture are also proposed.

La pêche des céphalopodes du golfe de Thaïlande porte sur des poulpes, calmars, seiches et nautiles cloisonnés qui représentent 8 familles, 14 genres et 24 espèces. Les calmars et seiches d'importance commerciale sont, respectivement: *Loligo formosana, L. duvaucelii, Sepioteutis lessoniana*, et *L. tagoi; Sepia aculeata, S. pharaonis, S. lycidas, S. recurvirostra, S. brevimana* et *Sepiella inermis*. Les relations longueur-poids, le sex-ratio, la taille à maturité, la fécondité et le contenu stomacal de certaines espèces ont fait l'objet d'études au cours des dernières années. Les prises de céphalopodes qui étaient de 11 602 t en 1965 ont augmenté de façon constante jusqu'à un maximum de 93 694 t en 1977; la production fluctue depuis cette date.

Les calmars et les seiches sont surtout capturés au chalut de fond dans les eaux du large et au haveneau et au carrelet dans les eaux côtières et semi-côtières. La pêche hauturière fait appel au chalut à panneaux et au chalut bœuf. Les zones de pêche du calmar et de la seiche les plus productives sont situées dans la partie nord-ouest du Golfe de Thaïlande, aux endroits où la profondeur est en moyenne de 25 m.

Une estimation préliminaire du rendement soutenu maximal des stocks de calmar exploités par la pêche au chalut a donné une valeur d'environ 42 000 t. La possibilité de récolte de l'ensemble du stock, qui comprend des stocks non chalutables et des formes pélagiques, n'est pas connue pour l'ensemble du golfe. On ne connaît pas non plus les rendements potentiels en seiches et poulpes.

Les données biologiques disponibles pour chacun des groupes d'espèces sont insuffisantes à l'évaluation des stocks. On présente les principaux secteurs qui devraient faire l'objet de recherches.

On présente aussi les études qu'il serait nécessaire d'effectuer pour exercer une gestion rationnelle des pêches, de par, notamment, la réglementation des pêches traditionnelles, la mise en place de méthodes de pêche non traditionnelles et la mariculture.

Introduction

Fisheries are important in the national economy of Thailand and the products provide a highly nutritious and relatively cheap source of protein for many Thai people. In the past two decades fisheries have developed dramatically because of the introduction of efficient fishing gear such as purse seines, gill nets and bottom trawls. The bottom trawl fishery which began around 1962 is now a particularly highly developed fishery and has been mainly responsible for the spectacular increase in fisheries production in the past two decades. Rapid development of bottom trawl fisheries has placed Thailand among the ten major fishing nations of the world with a long distance fishing fleet comparable to those of developed countries. Since the development of this fishery the catch from inshore gear such as push nets, set bag nets and bamboo stake traps has become negligible.

Bottom trawls not only catch demersal fish but pelagic fish and some invertebrates such as cephalopods and shrimp. In recent years the catch of cephalopods has contributed substantially to the income of trawlers; it is usually about 10% of total annual trawler landings. In 1979, production of cephalopods was 80 142 t with a value of 1 248 baht ($54 million U.S.).

More than half of this catch was exported either frozen or dried, the remainder was consumed locally.

The present paper summarizes information on the biology and fisheries for cephalopods in the Gulf of Thailand.

Biological Studies of Cephalopods

Cephalopods caught in Thailand fisheries include octopus, squid, cuttlefish, and chambered nautilus. Sithikorakul (1978) listed 8 families, 14 genera and 24 species that occur in the Gulf of Thailand (Table 1). Commercially important squid are: *Loligo formosana, L. duvaucelii, Sepioteutis lessoniana, L. tagoi*. Commercially important cuttlefish include *Sepia aculeata, S. pharaonis, S. lycidas, S. recurvirostra, S. brevimana* and *Sepiella inermis*. Surveys carried out by the Invertebrate Fisheries Investigation Unit (Anon. 1979) showed these species are common and widely distributed in the Gulf of Thailand. *S. aculeata* and *S. inermis* are found mostly at depths from 10 to 19 m, *S. brevimana* at depths from 40 to 49 m. *Loligo* and *Octopus* spp. are usually found at depths from 20 to 29 m. *S. lycidas* is only found in the southern part of the Gulf of Thailand (Sin-anuwong 1979).

Biological information on some species of squid and cuttlefish is summarized in Table 2. This information suggests that squid and cuttlefish spawn year around but that there are two spawning peaks, one in the early part of the year and another about the middle of the year. The fecundity of both squid and cuttlefish is similar; the number of eggs per female can range from 900–2000 depending on species and size. Larger species and larger sized animals usually have a greater number of eggs. The sex ratio of most squid and cuttlefish is similar, with fewer males than females.

TABLE 1. Cephalopods of the Gulf of Thailand (after Sithikorakul, 1978).

Family	Species
Argonautidae	*Argonauta boettgeri* Maltzan
Octopodidae	*Cistopus indicus* (d'Orbigny)
	Hapalochlaena maculosa (Hoyle)
	Octopus dollfusi Robson
	Octopus horridus d'Orbigny
	Octopus membranaceus Quoy & Gaimard
	Octopus parvus (Sasaki)
	Octopus spp.
Sepiadariidae	*Sepiadarium* sp.
Sepiidae[a]	*Sepia aculeata* Ferussac & d'Orbigny
	Sepia brevimana Steenstrup
	Sepia lycidas Gray
	Sepia pharaonis Eherenberg
	Sepia recurvirostra Steenstrup
	Sepiella inermis (Ferussac & d'Orbigny)
Sepiolidae	*Euprymna stenodactyla* (Grant)
Spirulidae	*Spirula spirula* (Linnaeus)
Loliginidae[a]	*Doryteuthis singhalensis* (Ortman)
	Loligo duvaucelii d'Orbigny
	Loligo formosana Sasaki
	Loliolus rhomboidalis Burgess
	Loligo tagoi Sasaki
	Sepioteuthis lessoniana Lesson
Nautilidae	*Nautilus pompilius* Linnaeus

[a] Families of commercial importance.

Loligo feed mainly on fish and to a lesser extent on cephalopods and crustaceans (Table 2). Cuttlefish feed mainly on crustaceans and to a lesser extent on fish.

L. formosana is the largest squid found in the Gulf of Thailand reaching a maximum dorsal mantle length (DML) of 20 cm. *L. tagoi* is the smallest squid species. *S. pharaonis* is the largest cuttlefish species attaining a reported maximum length of 23.4 cm.

When the length(cm)-weight(g) relationship was examined it was found that weight of males and females is comparable when they are young. As they grow larger the weight of females is greater than that of males for animals of comparable size, which may be due to gonadal development in females.

Research studies have been done on the biology of some species of cuttlefish. *S. inermis* was reared in the laboratory and the life cycle determined (Boonprakob et al. 1977b). Females of this species laid from 200–1000 eggs at a time and have several cycles of egg maturation during their life span. Embryonic development occurs in 11–20 d and they reach sexual maturity in 70–80 d. Mating and spawning occur about ten days after they reach sexual maturity. Growth of this species can be described by a sigmoid curve. Age of cuttlefish could be determined by lines on the cuttlebone (Boonprakob et al. 1977b).

Mating behavior of the cuttlefish, *S. inermis* and the squid *Sepioteutis lessoniana*, was studied by Boonprakob et al. (1977a and b), and Nabhitabhata (1983). The two species have similar mating behavior. Males usually display a characteristic color pattern during courtship and mating but females do not display any color pattern.

Embryonic development of *Sepiella inermis* can occur at salinities from 20 to 32 ppt but is retarded at higher salinities, 36 ppt (Boonprakob et al. 1977a and b). Adults of this species survived in salinities from 22 to 32 ppt. The optimum salinity for growth of *S. inermis* was from 28 to 32 ppt (Nabhitabhata and Polkhan 1983).

There is good potential for culturing several species of *Sepia*. The Sichang Marine Science Research and Training Station of Chulalongkorn University is studying the feasibility of culturing *S. pharaonis* in floating cages. This species can attain a large size and has a high commercial value.

Cephalopod Fisheries

FISHING GEAR AND AREAS

Cephalopod fisheries are among the most important fisheries in the Gulf of Thailand. Squid, cuttlefish and octopus are caught mostly by bottom trawls in offshore waters and by push nets and lift nets equipped with lights in the inshore and coastal waters of the Gulf.

Two types of bottom trawls are used in cephalopod fisheries, otter trawls and pair trawls. The two types of

TABLE 2. Summary of biological information of some cephalopod species found in the Gulf of Thailand, 1. Vipasiri (1980), 2. Ratana-anond (1980a), 3. Ratana-anond (1980b), 4. Ratana-Anond (1981), 5. Kitivarachet (1979), 6. Chotiyaputa (1980a), 7. Chotiyaputa (1980b), 8. Chotiyaputa (1980c). DML = dorsal mantle length.

Species	Fecundity (mean number of eggs female[1] and mature female size (DML cm) range)	Spawning season	DML(cm)-weight(g) relationship	Minimum DML length (cm)	Maximum DML length (cm)	Mean DML in catch (cm)	sex ratio (M:F)	Stomach contents (%)	Reference
Loligo formosana	2,015 (8.9–19.5cm)	all year with two peaks: Feb–May and Aug–Nov	M:$W = 0.007L^{1.87}$ F:$W = 0.003L^{2.09}$	—	20.0	M:10.0–11.9 F:10.0–10.9	0.61	fish 64.1% cephalopod 59.8% crustaceans 12.0%	1,2
Loligo duvaucelii	ave. 890 (7.5–11.5cm)	all year with two peaks: Feb–May and Aug.–Nov.	M:$W = 0.011L^{1.77}$ F:$W = 0.003L^{2.04}$	—	14.0	M:7.0–7.9 F:7.0–8.9	0.63	fish 60.2% cephalopod 56.5% crustaceans 10.7%	1,3
Sepioteuthis lessoniana	480–1,020 (15.7–18.5cm)	all year	M:$W = 0.001L^{2.36}$ F:$W = 0.001L^{2.40}$	—	18.0	M:9.0–9.9 F:6.0–6.9	0.40	fish 58.1% crustaceans 51.0% cephalopod 29.0%	1,4
Sepia aculeata	1,644	all year with two peaks: Mar–April and July–Sept.	M:$W = 0.001L^{2.49}$ F:$W = 0.001L^{2.60}$	M:7.0 F:8.1	16.9	M:6.0–6.9 F:5.0–6.9	0.80	crustaceans 73.7% fish 40.8% cephalopod 6.3%	6,7
Sepia pharaonis	1,868 (10.9–19.4cm)	all year with peaks in Jan. and July	M:$W = 0.001L^{2.61}$ F:$W = 0.001L^{2.61}$	—	23.4	M:9.0–9.9 F:6.0–7.9	—	crustaceans mostly	7,8
Sepia recurvirostra	570 (7.0–11.0cm)	all year with a peak in January	M:$W = 0.002L^{2.38}$ F:$W = 0.001L^{2.46}$	M:7.2 F:6.8	10.5	M:8.0–8.9 F:7.0–7.9	0.46	crustaceans 85.7% fish 21.9% cephalopods 6.7%	8,1

gear are used at different times of the day, otter trawls at night and pair trawls in the day. This practise produces a difference in catch composition. According to the 1979 statistics, catches from otter trawls were squid, cuttlefish and octopus in comparable proportions while the catch from pair trawls was mainly squid (Sin-anuwong 1979).

Cephalopod otter trawl fisheries are scattered along the east and west coasts of the Gulf of Thailand and can be divided into seven zones (Fig. 1). Pair trawlers operate in a more restricted area in three zones (A–C) at the northern end of the Gulf (Fig. 2). The most productive cephalopod fishing area is in the northwestern part of the Gulf from Prachuap to Samut Songkhram province (Sin-anuwong 1980).

Otter trawlers are usually 14–18 m in length, are equipped with engines ranging from 60 to 159 hp and have a crew size from 5 to 10 people. The width of the mouth of trawl nets is 22 to 34 m.

Pair trawlers are usually 18 to 25 m in length and are equipped with engines of more than 180 hp. Each boat has a crew of 13–25 people. The width of the mouth of the net ranges from 30 to 36 m.

LANDINGS

Cephalopod landings usually account for about 10% of total trawler landings. Harvest of cephalopods from the Gulf of Thailand increased from 11 602 t in 1965 to a peak of 93 694 t in 1977 (Table 3). Since then production has fluctuated but has shown a declining trend. The 1980 value of cephalopod production was about $1 000 million baht ($43.85 million U.S.).

It is not clear why production increased after 1969 but it may have been largely due to increased fishing effort, i.e. an increase in the number of trawlers in the Gulf of Thailand. A reduction in the number of cephalopod predators in the Gulf through various fishing operation may have produced a high survival rate of cephalopods and also lead to increased landings.

More than half the annual squid and cuttlefish production is exported either frozen or dried, mainly to Japan. The export value is much higher than landed value. In 1982 the exported value of squid and cuttlefish was about 26% of the total export value of fishery products (Table 4).

According to statistics for the 10-yr period 1971–80

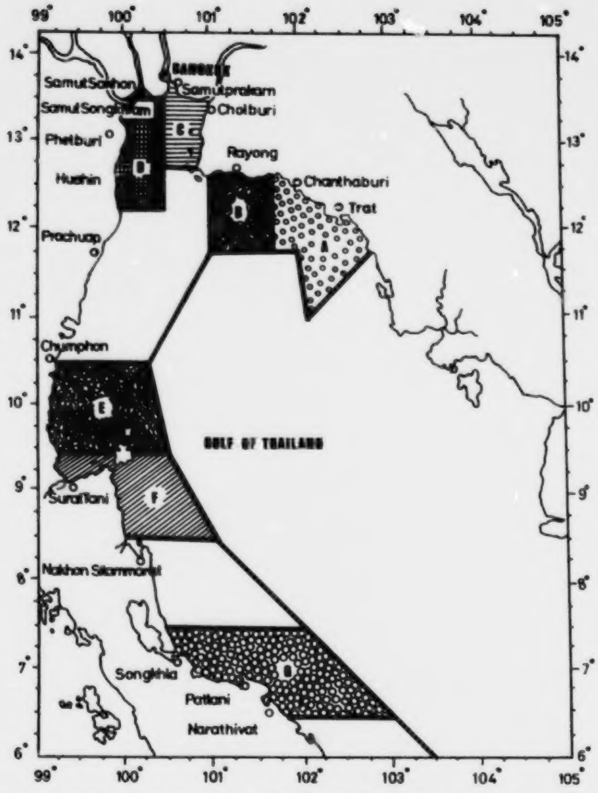

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FIG. 1. Fishing areas for cephalopods by otter trawlers in the Gulf of Thailand, 1979 (after Sin-anuwong 1979).

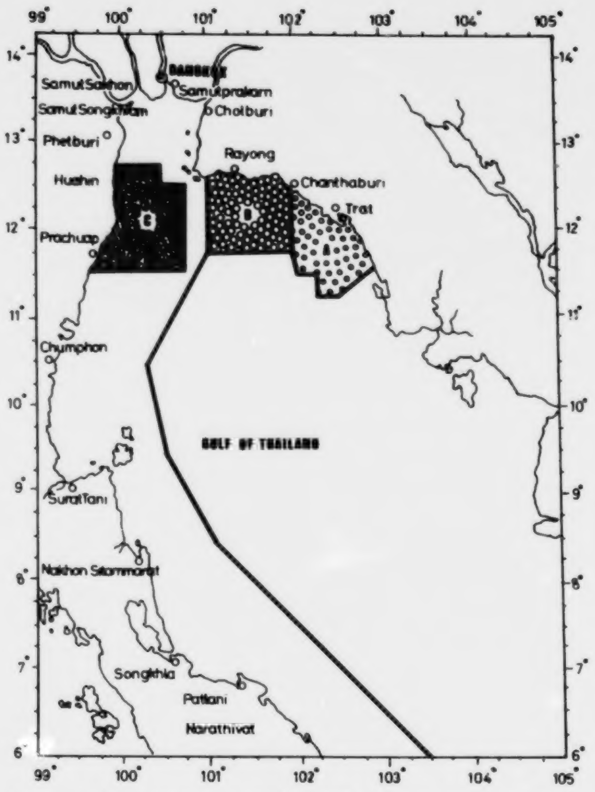

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FIG. 2. Fishing areas for cephalopods by pair trawlers in the Gulf of Thailand, 1979 (after Sin-anuwong 1979).

cephalopod landings were 57.7% squid, 36.3% cuttlefish, and 6.0% octopus (Table 3). *L. formosana* and L. duvaucelli were the dominant squid species landed. Figure 3 shows the variation in squid catch as a percentage of the total monthly catch of invertebrates in 1979. Monthly harvest of *L. formosana* was always higher than that of the three other squid species. Squid production was higher in the first half of the year than in the second half.

S. aculeata was the dominant cuttlefish species landed. Figure 4 shows variation in cuttlefish landings as a percentage of total monthly invertebrate landings in 1979. Monthly cuttlefish harvest did not vary significantly during the course of the year.

Vipasiri (1980) used Schaefer's model to calculate maximum sustained yield of squid resources in the Gulf of Thailand and estimated the MSY at about 41 965 t with an optimum fishing effort of 6.29 million hours (Fig. 5). The MSY of cuttlefish has not been determined.

These estimates of MSY indicate that exploitation of squid resources, particularly those in the 0–50 m depth range in the Gulf of Thailand, have been intense. There is evidence of overfishing, e.g. the significant reduction in catch per unit effort. It is believed there are additional squid resources available for development beyond the 50 m depth contour, but it would require different gear to harvest these resources since existing trawling gear is unsuitable for fishing these area. The calculated MSY is limited to trawlable stock, and total potential yield of squid in the Gulf, from both trawlable and non-trawlable (hard bottom and midwater) areas, is not known.

No assessment of cuttlefish and octopus stocks have been carried out in the Gulf of Thailand. Fragmentary information on these resources obtained from by-catches in the trawl fishery suggests a substantial resource of these cephalopods exists in the entire Gulf of Thailand.

FISHERY REGULATIONS

The Ministry of Agriculture and Cooperatives issued a Ministerial Notification on July 20, 1972 prohibiting the use of trawl nets and various other gear, such as push nets and shrimp nets from motorized fishing boats, within 3 km of the shoreline and within a radius of 400 m of stationary gear that has been licensed by the Department of Fisheries in seas or bays of coastal provinces. This regulation was introduced partly to protect juvenile stages of several marine species in coastal waters and also to avoid conflict between inshore, subsistence fishermen and trawlers.

It is apparent that present trawl fishery regulations are not stabilizing the fishery; the major cause of the recent decline in abundance of cephalopods in the Gulf of Thailand seems due to extensive fishing. Over-fishing has been recognized as a problem since 1968 by research workers of the Department of Fisheries (Menasveta 1980). The Trawl Committee established by the Department of Fisheries recommended urgent

TABLE 3. Landings and total value of squid, cuttlefish, and octopus in the Gulf of Thailand from 1965 to 1980 in tonnes. 1 U.S. dollar = 22.80 baht.

Year	Squids	Cuttlefish	Octopus	Total	Values (Million Baht)
1965	—	—	—	11 602	—
1966	—	—	—	13 845	—
1967	—	—	—	18 452	—
1968	—	—	—	21 650	—
1969	—	—	—	22 587	—
1970	—	—	—	41 315	—
1971	23 528	13 253	740	37 521	202.6
1972	44 691	23 920	4 222	72 833	326.5
1973	37 470	22 196	1 556	61 222	351.3
1974	42 051	20 938	1 641	64 630	355.9
1975	37 191	24 516	3 121	64 828	427.4
1976	36 163	23 753	4 036	63 952	559.9
1977	52 158	34 088	7 448	93 694	820.4
1978	52 117	34 494	7 043	93 654	1 184.6
1979	42 407	30 569	7 166	80 142	1 247.9
1980	39 017	28 412	4 884	72 313	1 001.0
Average 71-80	40 679	25 614	4 186	70 469	—
Ratio (%)	57.7	36.3	6.0	100	—

SOURCE: Fisheries Record of Thailand, 1963-80, Department of Fisheries, Ministry of Agriculture and Cooperatives.

TABLE 4. Export of principal fishery products of Thailand, in tonnes and million baht 1980-83, (1 U.S. dollar = 22.80 baht).

Fishery Products	1980		1981		1982		1983[a]	
	t	Baht ×10³	t	Baht ×10⁶	t	Baht ×10⁶	t	Baht ×10⁶
Frozen Shrimp	17 915	1 981	19 922	2 132	20 396	2 764	15 383	2 415
Frozen Squids & Cuttlefish	38 640	1 301	39 703	1 328	42 686	1 782	29 159	1 246
Fried Squids & Cuttlefish	2 454	378	2 913	487	3 096	554	2 222	419
Fish Meal	114 343	972	115 441	1 440	83 105	701	71 789	594
Canned Seafood	31 892	1 620	49 000	2 510	65 969	3 183	52 903	2 820
Total		6 252		7 897		8 984		7 494

[a] Jan.-Aug.

SOURCE: Thai Customs Department.

management measures including limited entry to the trawl fisheries in the Gulf of Thailand. These recommendations are being studied by Thailand authorities at the present time.

Summary and Future Requirements

Cephalopod resources are abundant and widely distributed in the Gulf of Thailand and landings are mainly from the trawl fishery. Exploitation of these resources has increased markedly since the mid 1960's due mostly to the increased value of cephalopods, but also because of a serious decline in catches of some demersal fish species. Cephalopod resources on non-trawlable bottom and in the upper regions of the water column have scarcely been utilized. However, squid stocks exploited with existing gear appear to be fully exploited, and possibly overexploited, at present. It is therefore unlikely that a further increase in effort in the trawl fishery would achieve greater sustainable catches of squid. Research is being undertaken to develop a fishery for squid resources on non-trawlable bottom by attracting them with lights and cathing them with dip nets.

The commercial importance of cephalopod products continues to increase and they are now important export products of Thailand. Further research is urgently required to determine optimum fisheries levels. The complete taxonomic identification of species in cephalopod catches is not possible at present, and biological information on octopus is virtually nonexistent in spite of the fact that they account for 5-10% of the cephalopod catch. Additional information on distribution, migration, spawning, growth, maturation, feeding and behaviour is needed for the rational utilization of cephalopod resources in the Gulf of Thailand. Studies on management options for cephalopod resources

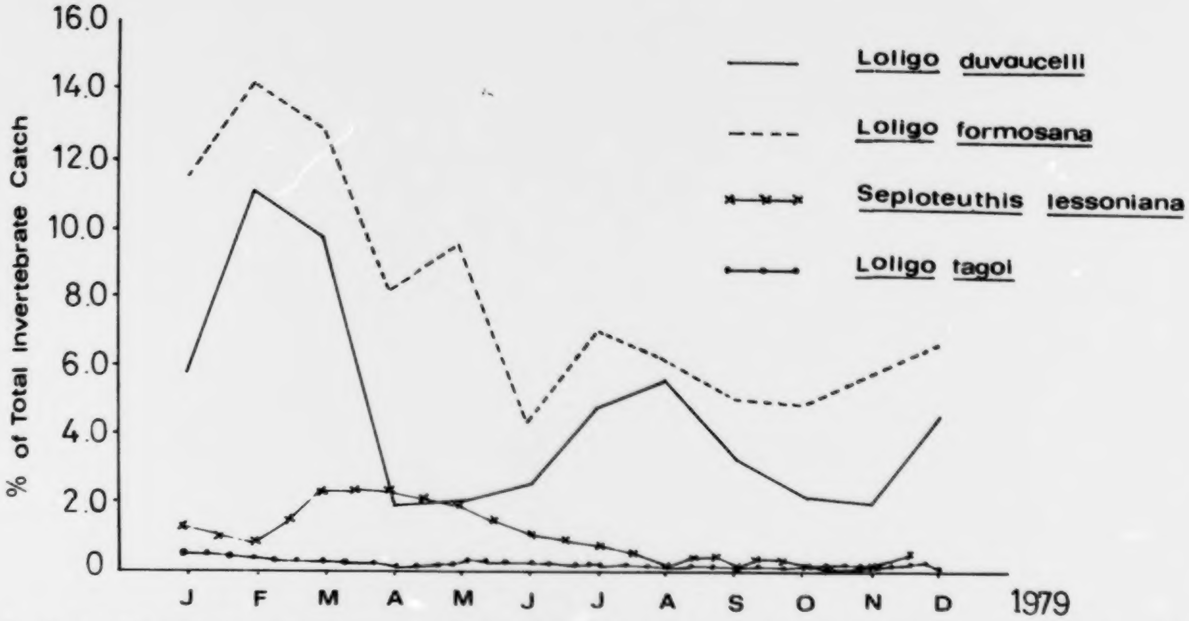

FIG. 3. Monthly production of four species of squid in 1979 in the Gulf of Thailand expressed as a percentage of the total invertebrate catch.

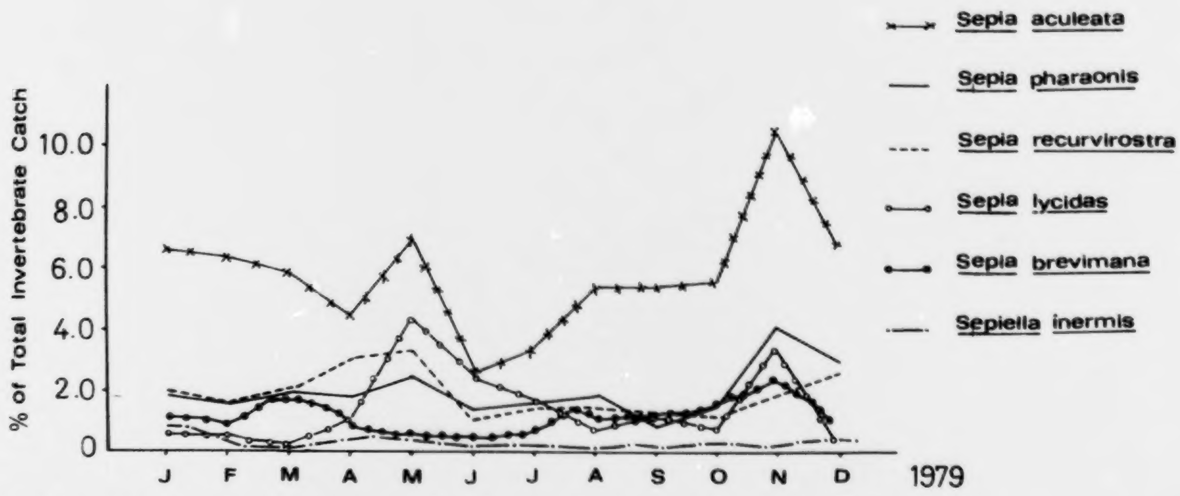

FIG. 4. Monthly production of four species of cuttlefish in 1979 in the Gulf of Thailand expressed as a percentage of the total invertebrate catch.

should also be intensified in preparation for the regulation of traditional fishing methods, e.g. trawls.

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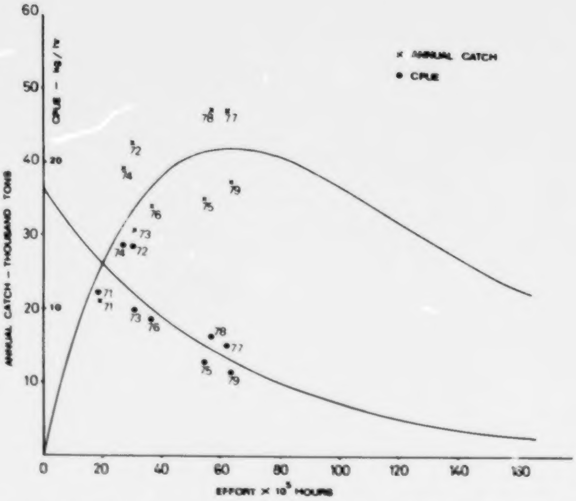

FIG. 5. Annual catch and catch per unit of effort of squid by commercial fishing as related to effort in the Gulf of Thailand (after Vipasiri 1980).

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MANAGEMENT STRATEGIES AND OPTIMIZATION OF YIELD

Management of the British Columbia Fishery for Northern Abalone (*Haliotis kamtschatkana*)

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Management of the British Columbia fishery for northern abalone (*Haliotis kamtschatkana* Jonas), population dynamics, and behaviour of the stock are described. The fishery exploded in 1976 after a long period of low-level sporadic fishing. Managers tried to reduce landings and effort first by limiting season length and restricting entry. These actions reduced neither landings nor effort, and may actually have intensified the fishery. An explicit annual quota was then imposed based on biological measurements, but by then the fishery had decreased the stock by 75%. Studies are reported which show that growth is slow (at least 6 yr are required for settlers to recruit), natural mortality rates are low, and recruitment rates are low. Stock reduction analysis was used to estimate fishing mortality rates and the virgin stock; such analysis demonstrated a recruitment failure. The low estimated recruitment was probably not caused by the fishery, but unstable recruitment makes choice of a management strategy difficult. Management strategies are explored with yield-per-recruit and egg-per-recruit analyses, and the results are discussed with reference to the general problem of managing gold rush fisheries.

Le présent rapport décrit la gestion de l'exploitation de l'ormeau pie (*Haliotis kamtschatkana* Jonas), la dynamique des populations et le comportement des stocks. En 1976, cette exploitation a pointé après une longue période d'activité sporadique de faible envergure. Les gestionnaires ont tenté de réduire les débarquements et l'effort en limitant premièrement la durée de la saison et le nombre de participants. Ces mesures n'ont pas eu l'effet recherché et de fait, peuvent avoir contribué à l'intensification de l'exploitation. On a ensuite imposé un contingent annuel formel d'après des quantifications biologiques mais le stock avait déjà chuté de 75 %. L'auteur mentionne des études qui révèlent que la croissance est lente (il faut au moins 6 ans avant que les animaux fixés atteignent la taille de capture), que les taux de mortalité naturelle sont faibles et que les taux de recrutement sont peu élevés. Il utilise une analyse de réduction des stocks pour calculer les taux de mortalité par pêche et le niveau d'abondance du stock vierge; de telles analyses ont révélé une faillite du recrutement. Le faible recrutement calculé n'est probablement pas le résultat de l'exploitation; un recrutement instable rend toutefois difficile le choix d'une stratégie de gestion. Des analyses du rendement par recrue et de la production d'œufs par recrue sont utilisées pour l'étude de stratégies de gestion et les résultats sont discutés relativement au problème général de gestion de pêches considérées comme des mines d'or.

Introduction

Haliotid gastropods support valuable fisheries in many parts of the world (see Mottet 1978; Harrison 1975 for reviews). Common features of these fisheries seem to be slow growth of species fished, low mortality rates, large accumulations of old individuals, and high product value. Because of these features, abalone stocks seem vulnerable to rapid depletion.

The British Columbia fishery for northern abalone (*Haliotis kamtschatkana* Jonas) is small compared with other abalone fisheries (Fedorenko and Sprout 1982). For several years, however, this fishery was the second most valuable shellfish fishery in B.C. Managers attempted to regulate the fishery for continuing yield almost from the beginning, and management history of this fishery is well documented. Despite this, management of this fishery was not entirely successful.

This paper examines behaviour of the British Columbia abalone stock during the course of this fishery, discusses effects of several management actions, and considers which management tools are most useful in regulating this and similar fisheries.

History of the fishery

The commercial fishery essentially began in 1976. Native Indians used abalone from the intertidal zone, but Thompson (1914) wrote: "The Indians appear to have had but few dealings with it . . ." In the first half of this century, immigrants used intertidal stocks to supply oriental markets (Thompson 1914; Quayle 1962); these appear to have been small and temporary ventures. From 1952 to 1975, when diving equipment became steadily better and more available, reported landings varied highly from year to year and were small compared with the post-1975 period (Federenko and Sprout 1982; Sprout 1983). Areas which supported landings also shifted considerably, suggesting short-lived local enterprises.

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In 1976 the fishery rapidly expanded for a number of reasons. These include development of a market in Japan, discovery of dense abalone beds in remote places, structural changes within the fishing industry, and advances in diving technology. Biological knowledge was limited to the work of Quayle (1971), who had studied growth rate, population size structure, and reproductive biology. Nothing was known about stock size, population density, or sustainable yield. Fishery managers, alarmed by the suddenly increased landings, closed the 1976 fishery in order to rationalize management. Subsequent management actions are described by Federenko and Sprout (1982) and are briefly summarized in Table 1. The management history of the fishery has two phases. From 1976 through 1978 sustainable catch levels were not known, and managers were concerned that catches seemed too high. Management actions attempted to prevent further expansion of the fishery by limiting entry, and to reduce catches by reducing season length and limiting effort per licence. These measures were not successful: catches rose significantly in 1977 and remained high in 1978 (Fig. 1). In the second phase, preliminary estimates of original stock and turnover rate had become available (Breen 1980), and managers introduced an annual quota in 1979 based on these estimates. Allocation of the total quota among individual licences was also introduced in 1979 for economic and social considerations. With the shift in management strategy from controlling effort and efficiency to controlling catch, season lengths and effort per licence were freed from restriction.

A minimum size limit 63.5 mm (2.5 in) measured across the shell was introduced in 1949 for unrecorded reasons. This was changed to 101.6 mm (4 in) length in 1977 (a small increase) and in 1980 was changed to 100 mm. However, the size limit was not considered a major management tool. Areas were closed for a variety of reasons such as resolving conflict between commercial and other users (Federenko and Sprout 1982). The effect since 1976 has been to reduce the total area available to fishermen.

Catch of abalone by groups other than the commercial fishery cannot be estimated. Pilot studies of recreational impacts on shellfish (McElderry, pers. comm.; Carmichael, pers. comm.) support the previous view (Breen 1980) that recreational use has been small compared with commercial catches.

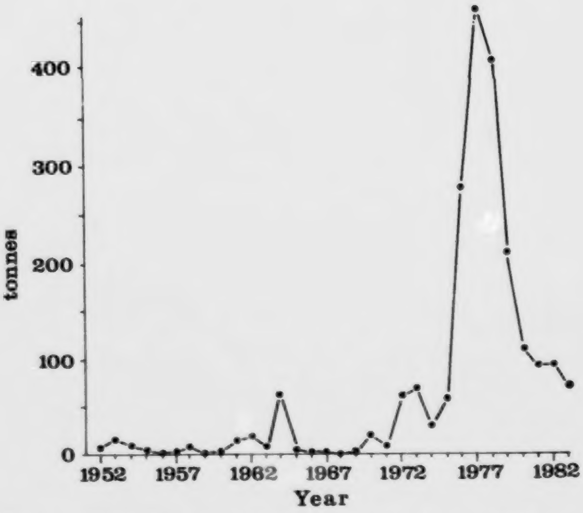

FIG. 1. Abalone catches, 1952–80. Catches before 1977 are from the sales slip system; subsequent catches are from logsheets supplied by fishermen.

Dynamics of Abalone Populations

This section will describe behaviour of the stock from 1976 through 1983. "Stock" is defined here as legal sized abalone in all areas open to the fishery. More than one functional unit stock may exist within this area, but in the absence of better information on stock identity one "stock" is assumed. Areas supporting commercial catches are shown in Fig. 2.

To reconstruct stock behaviour the method of Kimura and Tagart (1982) was used. The inputs to this method are an estimate of stock reduction since the beginning of the fishery, an estimate of natural mortality rate, and a record of catches. Stock reduction was estimated by comparing an estimate of pre-1976 density with later survey estimates. The species cannot be aged (Mottet 1978), so natural mortality rate was estimated from size frequency distributions using growth information obtained from tagging. Recruitment, not directly used in the procedure, was also estimated from size frequencies and growth information. Each of these estimates is described in detail below.

TABLE 1. Summary of major management actions and regulations respecting the abalone fishery, 1975–82 (modified from Federenko and Sprout 1982).

Year	Licensing (# licenses)	Season length (mo)	Quota (t)	Effort limit (divers/boat)	Size limit (mm)
1975	unlimited (21)	12	none	none	63.5[a]
1976	unlimited (43)	10.5	none	none	63.5[a]
1977	limited (29)	8	none	3	101.6
1978	limited (27)	3	none	3	101.6
1979	limited (26)	7	226.8	3	101.6
1980	limited (26)	7.5	113.4	none	100
1981	limited (26)	7.5	113.4	none	100
1982	limited (26)	7.5	113.4	none	100

[a] Measured across the shell.

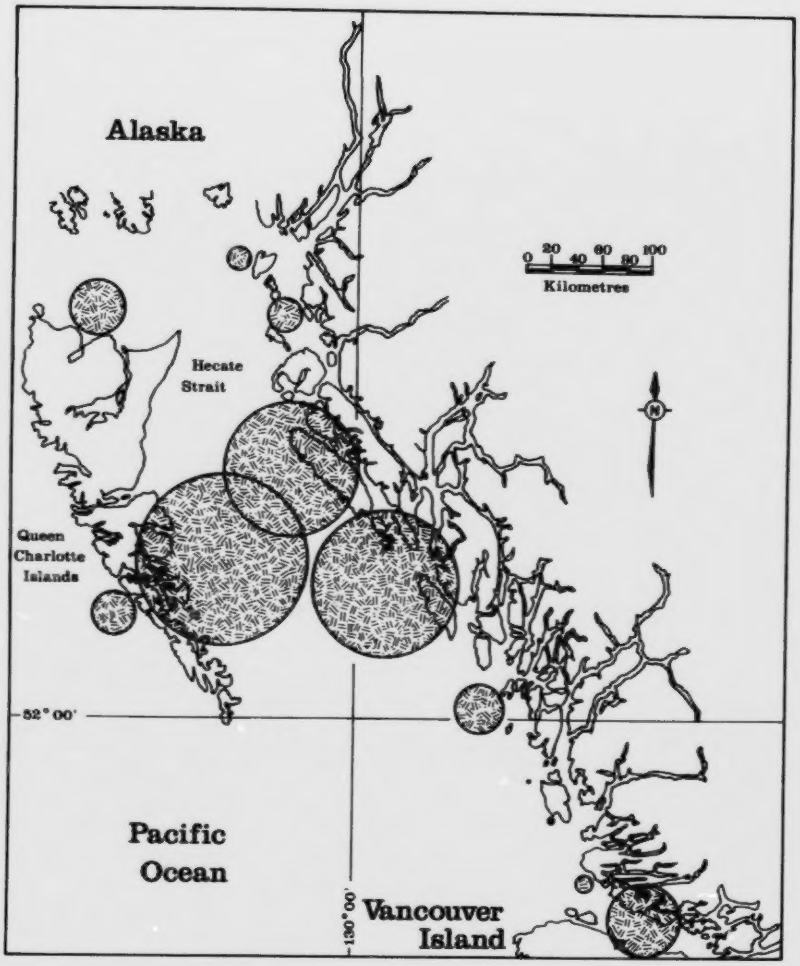

FIG. 2. Northern British Columbia coast, showing areas supporting major abalone landings. Areas of circles are proportional to catches, 1977–79, reported on logsheets supplied by fishermen.

STOCK REDUCTION

Direct estimates of abalone abundance are impractical because of the size of the B.C. coast and distribution of abalone along it. To examine changes in abundance, Breen (1980) considered mean density to be an index of abundance. He developed a standard method for measuring abalone density at a site. This consists of a procedure for finding sites, a procedure for placing 16 quadrats, 1 m², at each site and counting and collecting all abalone found in them. This method was used to measure density in a number of surveys from 1978 to 1984 (Boutillier et al. 1985, 1984; Breen and Adkins 1982, 1981, 1980, 1979; Breen et al. 1982). In the results presented here, density estimates from sites with legal sized abalone are considered to be a random sample from the population of all sites containing the stock.

The first estimates of abalone density were made only in 1978, after the intensive fishery had begun. To estimate the 1976–78 decrease in abalone abundance, Breen (1980) described four procedures. These were examination of changes in catch per unit effort, comparison of 1976 density estimates with later estimates at the same sites; examination of changes in population size structure between 1964 surveys (Quayle 1971) and 1978; and direct estimation of pre-1976 density from anecdotal sources.

Catch per unit effort, measured as catch per diver day reported on logsheets submitted by fishermen, showed a slight decline from 202 to 187 kg/d between 1977 and 1978 (Fedorenko and Sprout 1982). The tendency for catch per day to remain constant probably reflects a number of processes. Through learning, divers may become more efficient at choosing sites and finding abalone under water. Effort per diver day may increase because of increased competition among fishermen. The progressive discovery and exploitation of unharvested beds during the early phase of the new fishery also causes this effect (Harrison 1983).

Direct comparison of densities at 5 sites surveyed in both 1976 and 1978 indicated a decrease of 62%. Information provided by fishermen and early resarchers, and densities in unfished sites, suggested that pre-1976 density of legal-sized was 2.5/m² (Breen 1980). Changes in the relative abundances of legal-sized and sublegal sized abalone observed in 1964 and 1978 indicated a reduction of 57% in legal sized abalone (Breen 1980). Each of the three procedures just described has problems. Since each yielded similar results, however, it was concluded that pre-1976 density of legal-sized abalone was 2/m^2.

Mean densities of abalone observed during major surveys 1978–84 are summarized in Table 2. Based on a 1978 survey in the Queen Charlotte Islands (Breen and Adkins 1979) mean density of legal-sized abalone decreased from the pre-1976 2/m^2 to 0.56/m^2; a decrease of 72% during the first 3 years of the fishery. Similar density was observed at the same time in eastern Hecate Strait (Table 2).

TABLE 2. Mean densities (#/m^2) of abalone observed during major surveys from 1978 to 1984.

Place	Queen Charlotte Islands		Eastern Hecate Strait	
Date	1978	1984	1979–80	1983
# sites	66	70	22	32
Total abalone				
Mean density	2.53	0.65	2.86	1.91
SE	0.32	0.08	0.38	0.35
95% limits	1.90–3.16	0.50–0.80	2.12–3.61	1.23–2.59
Legal abalone				
Mean density	0.56	0.10	0.62	0.31
SE	0.07	0.02	0.10	0.06
95% limits	0.43–0.69	0.06–0.14	0.42–0.81	0.23–0.40

Surveys carried out in 1983 and 1984 showed significant decreases in both total abalone and legal-sized abalone in the two major areas examined (Boutillier et al. 1985, 1984). The apparent decrease in legal-sized abalone was 50% in eastern Hecate Strait from 1979 to 1983 and 82% in the Queen Charlotte Islands from 1978 to 1984 (Table 2). These studies indicate that present stocks may be near 10% of their pre-1976 abundance.

GROWTH RATE

In several marking studies, abalone were marked with individually numbered tags, shell length was measured to the nearest millimetre, and abalone were then released where they had been collected. As many as possible were recovered approximately 1 year later. This procedure was carried out at five sites (Table 3). Bauke Is. was chosen because it had been similarly used by Quayle (1971); the rest were chosen because they appeared to represent typical abalone habitat. At Ellis It. abalone were tagged with numbered Peterson disc tags attached to the shell with stainless steel wire threaded through two respiratory pores. At Bauke Is. abalone were tagged with Peterson disc tags cemented to the shell with waterproof epoxy putty. At the other three sites, abalone were tagged with numbered plastic "spaghetti" tags threaded through two respiratory pores and tightly knotted. Of these three tag types, the plastic spaghetti tags were quickest to apply, but suffered damage and loss from improperly tied knots and grazing by sea urchins. Peterson discs attached with wire probably suffered the least loss, but were slow to apply and may have caused disturbance after release (Harrison and Grant 1971).

Asymptotic length and the annual Brody coefficient were estimated from Ford–Walford plots of lengths at release and recovery (Ricker 1975). Length increments given by Quayle (1971) from similar experiments performed at three sites in the mid-1960's were also analysed (Table 4). The Brody coefficient varied from 0.158 to 0.505 among these sites, extremes being observed at sites with the fewest recoveries. Asymptotic length varied from 100.6 to 129.8 mm. A procedure for estimating growth parameters from population size frequencies (Schnute and Fournier 1980) was performed on lengths of abalone measured by Breen and Adkins (1979) at several sites characterized by bull kelp (*Nereocystis luetkeana*). Growth parameters were estimated to be $K = 0.216$ and $L_\infty = 132.8$ mm.

Results of a transplant growth experiment are also included in Table 4. This tested whether growth would change when individuals were moved between habitats. Abalone were taken from Hoskins It., measured, marked with "spaghetti" tags, and placed at Murchison Is.

TABLE 3. Geographic co-ordinates, dates and numbers of individuals marked and recovered in growth studies described in the text. The first three sites are reported by Quayle (1971).

Place	Lat. °N	Long. °W	Date released	Date recovered	No. released	No. legible recovered
Bauke Is.	48°51.9′	125°19.5′	25 Mar '64	10 Feb '65	—	31
Gilbert Is.	48°52.5′	125°19.6′	10 Feb '64	10 Feb '65	—	26
Sivart Is.	52°32.1′	131°35.6′	8 Jan '65	3 Feb '66	—	28
Ellis It.	48°51.7′	125°06.4′	25 Oct '76	10 Nov '77	327	24
Bauke Is.	48°51.9′	125°19.5′	3 Jun '77	25 May '78	340	26
Lyell Is.	52°38.4′	131°27.3′	16 Jul '79	31 Jul '80	1500	13
Newberry Cove	52°28.1′	131°26.9′	17 Jul '79	2 Aug '80	1000	34
Hickey Is.	52°59.6′	129°31.6′	29 Jul '80	14 May '81	1100	94
Murchison Is.	52°35.7′	131°27.7′	1 Aug '81	10 Jul '82	617	62
Hoskins It.	52°32.4′	131°32.8′	—	—	—	—

TABLE 4. Estimates of the Brody coefficient K and asymptotic length L_∞ in nine mark/recovery experiments described in the text and Table 3. Values in parentheses are 95% confidence limits.

Place	K	L_∞ (mm)
Bauke Is.	0.317 (0.103–0.580)	123.7 (118.8–128.5)
Gilbert Is.	0.204 (0.074–0.353)	137.3 (133.5–141.1)
Sivart Is.	0.230 (0.128–0.346)	129.8 (126.8–132.9)
Ellis It.	0.158 (0.00–0.434)	122.6 (116.1–129.1)
Bauke Is.	0.351 (0.234–0.483)	114.2 (111.0–117.4)
Lyell Is.	0.505 (0.366–0.668)	100.6 (98.2–103.0)
Newberry Cove	0.195 (0.144–0.249)	95.2 (94.6– 95.9)
Hickey Is.	0.241 (0.129–0.365)	113.8 (112.0–115.6)
Murchison Is.	0.267 (0.07–0.510)	124.2 (116.3–132.2)

(Table 3). Hoskins It. was a moderately exposed site, characterized by high abalone density and narrow beds of tree kelp (*Pterygophora californica*) (Breen and Adkins 1979). Fournier and Breen (1983) estimated from a population size frequency that growth rate was low at this site ($K = 0.20$, $L_\infty = 92.0$ mm). In contrast, Murchison Is. was sheltered and supported a low density of large abalone in wide beds of giant kelp (*Macrocystis integrifolia*). Growth shown by recovered individuals 1 year later, was $K = 0.267$ and $L_\infty = 124.2$ mm. Thus asymptotic length at Hoskins It. had apparently been limited by environmental conditions (exposure to surge and limited low quality food). The transplant showed that stunted abalone retain the potential to grow well when placed in a more favourable habitat.

POPULATION SIZE STRUCTURE

Size classes of abalone are not uniformly distributed by depth. Large individuals are most numerous in the sublittoral fringe of vegetation extending down to the upper limit of sea urchin barrens. They are least numerous in the broken rock fields found deeper of sea urchin barrens. Conversely, small individuals (<50 mm) were most abundant in the deeper broken rock and much less abundant in the vegetated section (Breen and Adkins 1979). These differences cannot be explained by differences in diver searching efficiency between the different substrates: divers took as long as required to search completely all the area encompassed by a quadrat.

These observations suggest that juvenile abalone settle in deeper water and migrate upward as they grow, or that settler mortality varies with depth. Samples were therefore obtained through stratified sampling in three zones: the kelp zone, the 10 m band immediately below the kelp, and in the contiguous deep zone. Zone widths were measured, and composite samples were constructed from the stratified subsamples (Breen and Adkins 1982).

Population size structures obtained this way are described by Breen and Adkins (1981, 1982); three examples are shown in Fig. 3. At Hoskins It. (Fig. 3a), the composite sample contains identifiable modes of several juvenile age-classes, and abundance decreases with age. At Huxley Island (Fig. 3c), the population consisted entirely of individuals greater than 60 mm, with the first mode at 100 mm. An intermediate situation was found at Lyell Is. (Fig. 3b). Situations such as that at Huxley Is.

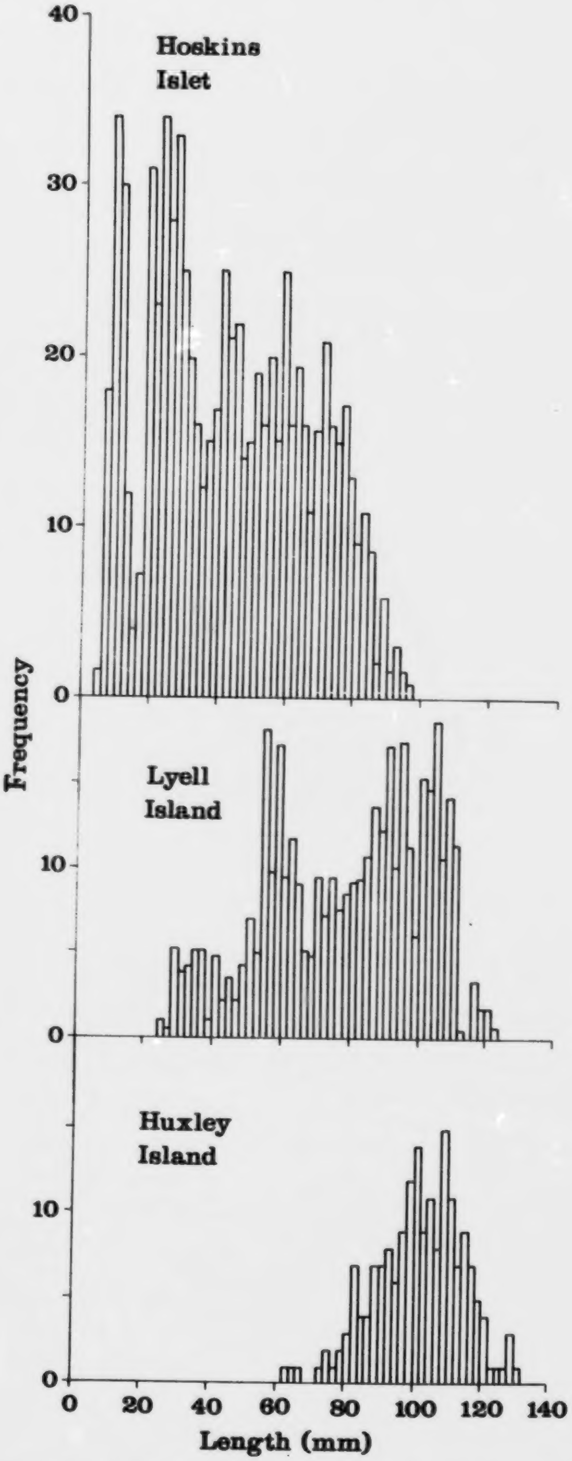

FIG. 3. Population size frequencies from stratified sampling at three sites. Detailed methods and site descriptions are given by Breen and Adkins (1982).

must have resulted from much better settlement or survival of juveniles in the past.

MORTALITY RATE

Mortality rate was estimated from population size structure and growth rate estimates (Fournier and Breen 1983). Growth parameters discussed above (Table 4) and population length frequencies from stratified sampling were used in this analysis. A problem with this method is that dynamics of local populations may not fit the assumption that recruitment to the sampled population varies around a stable value. This problem was addressed by varying the postulated number of age classes from 10 to 14, and varying the assumed age of the first age class fully available to the sampling procedure. If the estimated mortality rate varied by less than a factor of 2 over such variation, the sample was assumed to fit the assumptions of the model. Otherwise estimated rates were rejected.

Samples from 15 sites are shown in Table 5. Estimates from five sites were unstable. Remaining estimates of instantaneous total mortality rate ranged from $Z = 0.048 - 0.410$. The highest rates were estimated from sites exposed to the commercial fishery (Ramsay Is. and Hickey Is.), but at Ramsay Is. few sampled individuals were legal-sized. The remaining estimates, all from unharvested locations, are centred on about 0.15–0.20. These results are slightly lower than those obtained by Breen (1980) with the method of Van Sickle (1977) and Heincke (Ricker 1975). Sensitivity of mortality rate estimates to sampling error can be seen in estimates from Lyell Island, where nearly the same site was sampled in each of 4 consecutive years.

RECRUITMENT

Density of recruits to the fishery was estimated from survey results and growth rates. Breen (1980) calculated the length ranges of those individuals which would become legal size within a year ("pre-recruits"), and those which had become legal size within the past year ("new recruits"). These ranges were 94.0–101.6 mm and 101.6–107.0 mm, respectively. Densities of new recruits and pre-recruits from three surveys are shown in Table 6. Pre-recruits averaged 0.30/m², and new recruits 0.22/m². At equilibrium the density of new recruits (Rd) required to replace recruited individuals dying naturally would be:

$$\mathrm{Rd} = D\,(1 - \exp(-M))$$

where D is the density of already-recruited adults. The expected density of pre-recruits (PRd) would be

$$\mathrm{PRd} = \mathrm{Rd}\,\exp(M)$$

Using the pre-1976 density of 2.5/m² and $M = 0.20$, replacement densities of pre-recruits and new recruits are 0.55/m² and 0.45/m² respectively. Observed values (Table 6) are less. In addition, recruitment densities observed in 1983 and 1984 were much less than values previously observed in the same areas (Boutillier et al. 1985, 1984). Thus recruitment in 1978–79 was already less than that required to maintain pre-1976 levels of stock, and recruitment subsequently declined.

STOCK REDUCTION ANALYSIS

Original stock size can be estimated from the proportion by which a stock has decreased, catches from the stock, and assumptions about natural mortality, recruitment, and growth. Kimura and Tagart (1982) present a method in which n years of catch data are used to obtain solutions for the n equations of the form:

$$(1)\; B_i = B_{i-1}\,(1 - \exp - (F_{i-1} + M)) + R$$

where B_i is stock biomass at time i, F_{i-1} is instantaneous fishing mortality rate in year $i-1$, M is the constant rate of instantaneous natural mortality, and R is a constant recruitment biomass. Simultaneous solutions of F_i (i = 1, to n) and R are obtained while holding constant M, B_0 (the biomass at time 0), and the stock reduction P, where

$$(2)\; P = B_n/B_0$$

As P, M, and B_0 can be varied, there are many possible solutions to the set of n simultaneous equations. Kimura and Tagart (1982) suggest that, as a first approach, one can calculate replacement biomass for given values of M and B_0:

$$(3)\; R_R = B_0\,(1 - \exp(-M))$$

and then choose a solution in which estimated recruitment equals the replacement value. In the context of this method, "recruitment" includes actual recruitment of new biomass to the stock and growth of already recruited biomass (Kimura, pers. comm.).

This analysis was applied to abalone catches from 1975 to 1983 (Fedorenko and Sprout 1982; Sprout 1983; K. Bates, pers. comm.). Natural mortality rate was varied from $M = 0.15$–0.40; at each value of M, P was varied from 0.10 to 0.40; and at each value of P, B_0 was varied from 1100 to 2700 tonnes (t). An example is illustrated for $M = 0.15$ (Fig. 4). When $M > 0.15$ was used, there was no solution at which estimated recruitment was equal to replacement recruitment. Using $M = 0.15$, estimated recruitment approached replacement values as P increased, and as B_0 decreased. However, at low values of P there was still no solution at which R was equal to R_R; and at higher levels of P solutions were characterized by values of F that approached 1.0. Because mean size of the catch has remained well above minimum legal size (K. Bates, pers. comm.) such high fishing mortality rates cannot have occurred.

The pattern of variations can be summarized as follows: estimated recruitment approached replacement levels as M decreased, P increased, or B_0 decreased. The lowest value of M and the highest P consistent with evidence presented above are $M = 0.15$ (Table 5) and $P = 0.40$. At these values, the replacement solution involves unrealistically high values of fishing mortality rate during parts of the exploitation history. Because

TABLE 5. Total mortality rates estimated from population size structure at 15 sites. For site locations, descriptions and sampling methods see Breen and Adkins (1981, 1982). Ranges shown are extreme values obtained with the method of Fournier and Breen (1983), varying the number of age classes from 10 to 14 and the assumed age of the first age class fully recruited to sampling from 1 to 3. Asterisks indicate that estimates were unstable during this variation.

Site	Site #	Instantaneous total mortality estimates
Ellis It.	—	*
Anderson Is.	79-30	*
Hickey Is.	79-33	0.205-0.349
Bennett It.	79-39	0.127-0.244
Ralph Is.	79-40	0.161-0.182
Cumshewa Inlet	79-54	*
Kunga Is.	79-67	*
Lyell Is.	79-68	0.146-0.199
Weeteam Bay	80-69	*
Lyell Is.	80-71	0.048-0.090
Hoskins It.	80-73	0.139-0.207
Ramsay Is.	80-74	0.276-0.410
Lyell Is.	81-34	0.071-0.116
Newberry Cove	81-35	0.137-0.151
Lyell Is.	82-25	0.181-0.222

TABLE 6. Numbers of "pre-recruits" and "new recruits" observed during quadrat sampling in the years shown. "Pre-recruits" were defined as individuals with lengths of 94.0-101.6 mm; "new recruits" as those with lengths 101.6-107.0 mm. Replacement densities were estimated as described in the text, assuming 2.5 legal-sized individuals/m^2 and $M = 0.20$.

Year	# sites	# m^2	pre-recruits	#/m^2	new recruits	#/m^2
1978	45	746	198	0.265	175	0.235
1979	33	1416	489	0.345	357	0.252
1983	32	512	118	0.230	56	0.109
Total	110	2674	805	0.301	588	0.220
Replacement densities				0.554		0.453

replacement recruitment solutions cannot be obtained with realistic parameter estimates, one must conclude that recruitment has been less than replacement recruitment for this stock during the history of exploitation. This conclusion is consistent with the direct recruitment estimates presented earlier (Table 6), and with the shape of population size structures (Fig. 3).

A stock reconstruction from a plausible stock reduction analysis is shown in Fig. 5. In this example, from evidence presented earlier, $M = 0.20$, and $P = 0.25$. The original stock estimate was 1800 tonnes; stock was reduced to around 450 tonnes by the end of 1980. With estimated "recruitment" being less than replacement (estimated recruitment 180 t/yr; replacement recruitment 330 t/yr) the stock would have declined to about 1200 t in 1980 of its own accord. Estimated fishing mortality rates for 1976-80, respectively, were 0.18, 0.46, 0.66, 0.51, and 0.30.

It is unlikely that the fishery can have been the cause of reduced recruitment rates inferred from these results.

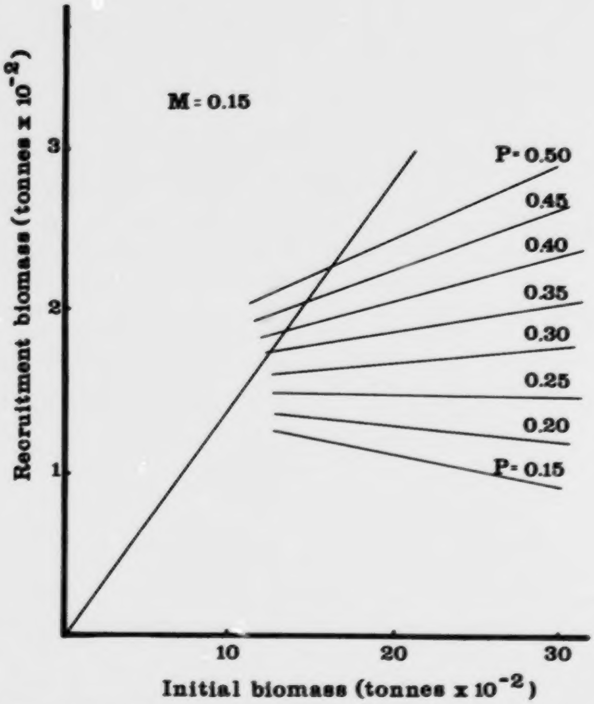

FIG. 4. Results of a stock reduction analysis (Kimura and Tagart 1982). Each point represents the estimated constant recruitment for a given value of B_0; each line connects points at which P was held constant at the value shown. The diagonal line from the origin connects points representing replacement recruitments. The natural mortality rate was held constant at $M = 0.15$. See text for further details.

From settlement to recruitment in this species requires at least 6 years, and the fishery has operated for only 8. If cohort strength is determined early in the life cycle, the strength of recruitments over the period discussed must have been determined before the fishery began.

YIELD-PER-RECRUIT AND EGG-PER-RECRUIT CONSIDERATIONS

Results from the previous section suggest that recruitment in this species may fluctuate independently of stock size. If there were no relation between stock size and subsequent recruitment, then the species could be managed to obtain the best yield from a cohort. This view is explored here with a yield-per-recruit analysis. Sluczanowski (1984) presents an analysis of reproductive output from Australian abalone under different fishing regimes. He showed that high fishing mortality rates sometimes led to very low reproductive outputs, and that egg production could be increased dramatically at a comparatively small cost in decreased yield. In this section a similar analysis is undertaken, and the consequences of combining yield-per-recruit and egg-per-recruit considerations are explored.

Yield-per-recruit analysis was performed using the method of Beverton and Holt (1957; Ricker 1975), with growth and mortality estimates from the results above. At the present rate of fishing ($F = 0.30$, estimated from stock reduction analysis) a better yield/recruit could be

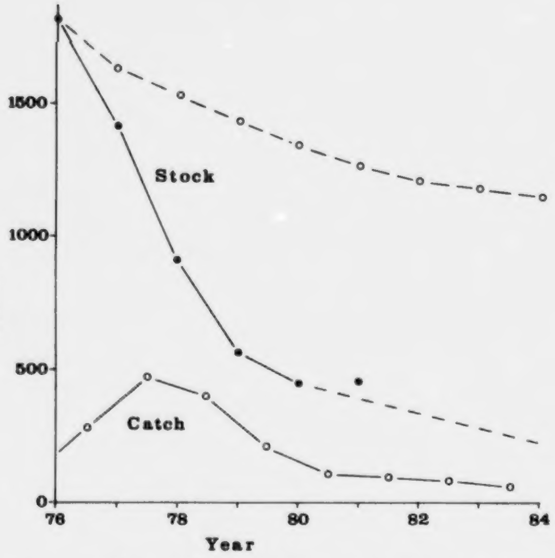

FIG. 5. A possible stock reconstruction based on a stock reduction solution. The solution was obtained with $M = 0.20$, $P = 0.25$, $B_0 = 1800$ t, using catches from 1976 to 1980.

obtained if the minimum size limit were slightly smaller than the present 100 mm limit (Fig. 6). The form of the isopleth diagram suggests two features that a management strategy could exploit. First, at rates of fishing $F < 0.20$, yield is nearly constant irrespective of size limit for size limits less than 100 mm. Second, at size limits greater than 110 mm and rates of fishing $F > 0.20$, yield changes little with increased fishing effort.

A simple model was developed to examine the production of eggs during the life of a cohort under different fishing conditions analogous with those examined in the yield-per-recruit analysis. Egg production was assumed to be a discrete event each year. The relation used was:

$$(4)\ E = \sum_{t=t_f}^{t=t_R} f_t N_0 \exp - (Mt) +$$

$$N_0 \exp(-Mt_R) \sum_{t=t_R}^{t=\lambda} f_t N_0 \exp(-Zt)$$

where E is the total number of eggs produced by N_0 females, t_f is the time at first maturity, t_R is time of recruitment to the fishery, t_λ is the maximum age attained, and f_t is age-specific fecundity. In the absence of published fecundity estimates for *H. kamtschatkana*, a curve of the form used by Poore (1973) was determined. The constants chosen described first egg production mean 50 mm length (Quayle 1971), and a fecundity of 2.3 million eggs at 135 mm shell length based on estimates by Scharlene Olsen (unpubl. data) and Kikuchi and Uki (1974, 1975). Fecundity (millions of eggs) was given by:

$$(5)\ f_t = (0.0065 \cdot w_t) - 0.098$$

where w_t is weight (g) at time t. Weight was calculated from length, in turn determined from a von Bertalanffy growth equation using the same parameters used for the yield-per-recruit analysis presented above.

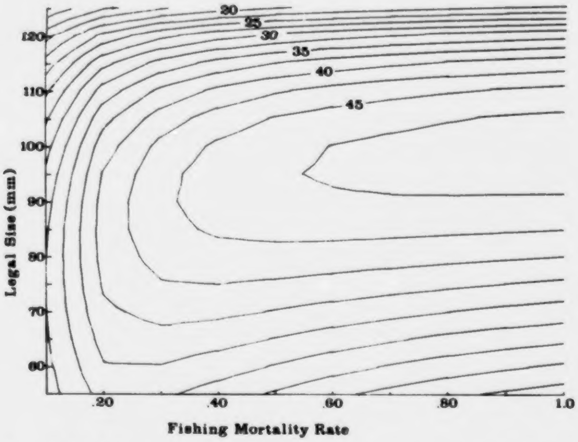

FIG. 6. Yield-per-recruit (g) as a function of minimum legal size and instantaneous fishing mortality rate, determined with the method of Beverton and Holt (Ricker 1975). Parameters were $M = 0.20$, $K = 0.25$, $L_\infty = 130.0$ mm. W_∞ was determined from length–weight relations presented by Breen and Adkins (1982).

Results (Fig. 7) are presented as a percentage of the maximum number of eggs produced by an unfished cohort. At low fishing mortality rates, egg production is nearly independent of size limit; at size limits above 100 mm and when $F > 0.20$, egg production is nearly independent of fishing mortality rate. The surface shows a large area of relative instability. For size limits <100 mm and $F > 0.20$, egg production is sensitive to changes in either parameter and is generally low. At the present size limit and fishing rate, a cohort can produce about 25% of its potential eggs. These specific results depend on the Poore curve used in the absence of data for this species. If the fecundity curve is similar (fecundity increases in close proportion to weight), the form of the results should be similar.

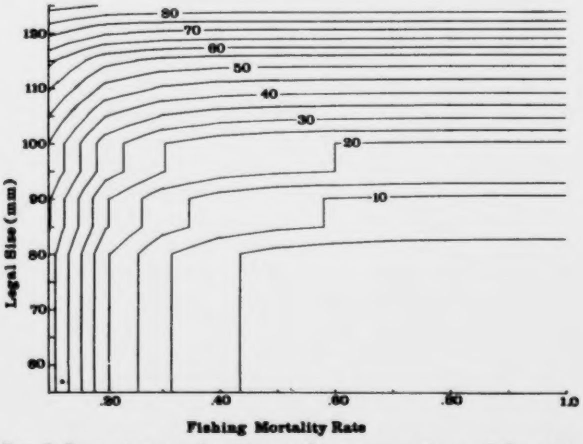

FIG. 7. Eggs per recruit, expressed as a percentage of the eggs that would be produced by an unfished cohort. See text for procedure. Parameters were all identical with those used in Fig. 6.

Without knowing what relation egg production bears to subsequent cohort strength, a manager cannot determine the desired level of egg production. However, if levels are determined either arbitrarily or as the result of analysis, it is simple to combine the egg production and yield-per-recruit strategies. The yield-per-recruit and egg-per-recruit surfaces could be combined into a strategy value:

(6) $S = YR/YR_{max}EPV$

where S is the relative value of a particular combination of size limit and fishing mortality rate, YR is yield-per-recruit, YR_{max} is the maximum yield-per-recruit possible, and EPV is an arbitrary function of E/E_{max} (range 0 to 100) chosen by the manager to reflect desirability of various levels of E. With the values used for this example, the surface of S values is shown in Fig. 8. The rectangular nature of the surfaces noted in the egg- and yield-per-recruit surfaces is also present here in stronger form. At size limits above 100 mm, strategy value changes little with fishing mortality rate. The surface contains a large area (where size limit is <100 mm and $F > 0.20$) over which relative strategy values are very low. In this example, the best strategy appears to be a combination of large size limit (120 mm) and $F < 0.40$.

Discussion

POPULATION DYNAMICS

Natural mortality rate of this species appears relatively low ($M = 0.15$–0.20). These estimates are consistent with observations of other species. Using a variety of techniques, several authors have estimated natural mortality rate in abalone to be within the range 0.5–0.30 (Smith 1972; Beinssen and Powell 1979; Sainsbury 1982a; Shephed et al. 1982). Other authors, using methods based partly on dead shell production, have obtained high estimates of mortality rates (Tutschulte 1973; Hines and Pearse 1982). A problem with these estimates is that dead shells may be more available to sampling than live animals, leading to over-estimates of mortality. Methods based on size frequency analysis, although they may have other problems, avoid this difficulty if availability of individuals to sampling is not size-specific.

In this study, growth estimates were consistent with those observed elsewhere. Growth has been well studied in abalone (see Sainsbury 1982a; Shepherd and Hearn 1983 for reviews). A common feature of abalone growth is variation with habitat and food quality (Leighton 1966; Kikuchi et al. 1967; Guzman et al. 1969; Breen 1980; Hirose 1974). Both recruitment and growth in *H. kamtschatkana* vary with habitat type (Breen and Adkins 1979), and growth and reproductive effort may vary with local disturbances in food supply (Tegner, pers. comm.). Such variation means that the use of an "average" growth rate is an over-simplification. To model the situation correctly, one should know growth and recruitment rates from a range of habitat types, and should also know the relative contributions of various habitats to landings. This is not practical in most situations.

Recruitment to the British Columbia stock of *H. kamtschatkana* appears to have declined from previous levels. Size frequencies show a paucity of juveniles, even when intensive stratified sampling eliminates possible sampling bias against small individuals. Direct estimates of the density of new recruits and pre-recruits are less than those required to replace the pre-1976 stock. The assumption of replacement recruitment is not compatible with stock reduction analysis. Reduced recruitment may have occurred independently of the fishery: abalone growing at the rates observed in tagging studies require at least 6 years to recruit after settling, but the evidence shows declining recruitment within five years of the beginning of this fishery.

Some historical evidence suggests that *H. kamtschatkana* in British Columbia demonstrated previous large variation in abundance. Quayle (1962 and pers. comm.) cites a 1955 commercial survey that found very low numbers of abalone. Data from that survey contrast markedly with results of surveys made in the same places by Thompson (1914), Quayle (1971), and Breen and Adkins (1979). In 24 Queen Charlotte Island sites, for instance, a diver found legal sized abalone at only six sites in 1955; Breen and Adkins (1979) found legal abalone at 66 out of 129 sites. A survey in southeastern Alaska (Livingstone 1952) also showed poor abalone stocks in the early 1950's. Differences in technique or observer experience cannot account for the difference between the 1955 and other surveys. Thus stock may have experienced at least one natural decline and recovery before the present fishery began.

Declines in settlement size or recruitment have been documented in two other abalone populations where a fishery was not implicated. Sainsbury (1977, 1982b) concluded that settlement of juvenile *H. iris* had declined from a previous level in an unfished study population. In the Channel Islands, *H. tuberculata* has had a series of population fluctuations, resulting in several fishery closures during the low phases (Stephenson 1924; Forster 1962; Bossy and Culley 1976; Clavier 1983). Hayashi (1980) showed that settlement is unstable. Forster et al. (1982) observed poor settlement of juveniles on Guernsey and the other islands, even in places not harvested by divers. They suggest that physical mechanisms account for declines in settlement.

These examples suggest that abalone have significant natural fluctuations in reproductive success. This is a common feature in many molluscs (Coe 1956; Hancock 1973). A usual speculation is that environmental variation affects some part of the reproductive process or the early life history (Wooster 1983). Prior to abalone settlement there are several opportunities for physical aspects of the environment to prevent the realization of full reproductive success (Leighton 1974); and these may be greater near the limits of geographical ranges (Hancock 1973).

MANAGEMENT STRATEGIES

The relevance of strong natural variation in reproductive success to the management strategy for a species such as abalone is not obvious. Such species may experience very good reproductive success and subsequent large recruitment from a relatively small spawning stock (Hancock 1973). In these cases the very high adult fecundity (especially in molluscs) may allow a small stock to exploit rare sets of favourable conditions (Hancock 1979). Thus in such species the stock–recruit relation appears poorly defined. A converse view is that species may adapt to unpredictability in reproductive success by developing long reproductive life histories (Comfort 1957; Goodman 1984). In abalone, having low adult mortality rates and high fecundity in large individuals, the relative reproductive value of old, large adults might be very high. This is shown by the impact of even light fishing on egg production (Fig. 7 and Sluczanowski 1984). According to this view, "recruitment overfishing" (Gulland 1973) can be caused by removal of a significant proportion of the stock. Recruitment overfishing has been suggested as a major cause of declines in the California abalone fisheries (Burge et al. 1975).

The strategy chosen for management of a species such as abalone depends on which view is accepted. If there were actually a poor underlying relation between stock and recruitment, then the management problem reduces to maximizing yield-per-recruit. Where yield-per-recruit analyses have been carried out on abalone populations, best yield occurs at high rates of fishing, and usually at minimum legal sizes slightly smaller than those already in place (Fig. 6; Ishibashi and Kojima 1979; Sainsbury 1977, 1982b). However, the strategy must be different if there exists a strong underlying stock–recruit relationship, even one that may often be obscured by environmental variation. Fishing rates and size limits that give good yields-per-recruit might result in very low egg production (Sluczanowski 1984) and could severely reduce recruitment. The form of the egg-recruit curve is unknown for abalone, so a manager has no a priori way to determine the level at which egg production should be maintained. Maximizing yield-per-recruit and maintaining some arbitrary level of egg production (Fig. 8) could be achieved using an appropriate minimum size limit as the major regulatory tool. A manager could choose upper and lower limits on desired egg production, construct a relation as shown in Fig. 8, and choose a minimum size corresponding to the chosen best compromise. As the shape of the surface in Fig. 8 shows, an appropriate size limit strategy can absorb large changes in fishing rate.

Management of abalone by size limit regulation does not have a good history. In California, it was thought that an appropriate size limit alone could maintain stocks (Heath 1925; Bonnot 1930; Cox 1962; Bissell and Hubbard 1968) but stocks have subsequently shown serious decline (Burge et al. 1975; Cicin-Sain et al. 1977). Size limits have been a major part of regulatory strategies in Japan (e.g., Ino 1966; Nonaka and Fushimi 1972; Mottet 1978) and the Channel Islands (Bossy and Culley 1976); but stocks have declined. The poor record in these cases might be the result of poorly chosen size limits. Inspection of Fig. 6 shows a large area, where high fishing pressure combines with low size limits, over which egg production is very low. Minimum sizes in this area may be appropriate from yield-per-recruit considerations, but could produce recruitment collapse. Another problem with minimum size limit is that when the ratio of legal sized to sublegal individuals becomes low, many sublegal abalone are picked from the rocks, measured and replaced. This conveys a high risk of injury or subsequent predation, and such mortality is blamed for some of the California fishery declines (Burge et al. 1975; Cicin-Sain et al. 1977).

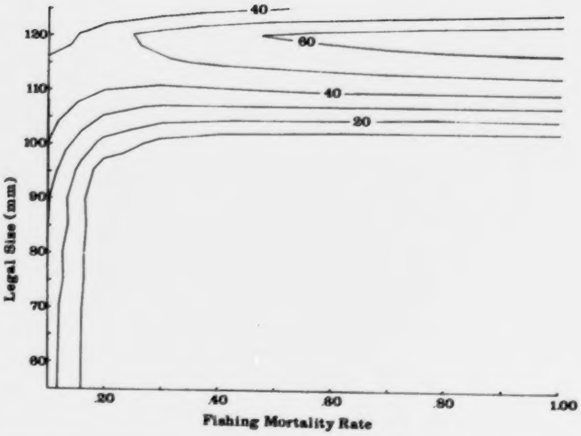

FIG. 8. Relative values of various combinations of minimum size limit and fishing mortality rate, using the procedure described in the text. Values have a range of 0–100; 100 representing maximum yield-per-recruit and at least 50% of possible egg production.

MANAGEMENT OF GOLD-RUSH FISHERIES

The fishery for *H. kamtschatkana* is typical of new fisheries for valuable species. Their rapid development has led to the term "gold-rush" fisheries (Hancock 1979), and can be caused by new markets (especially specialized export markets), new technology, or the discovery of new stocks of an exploitable resource. The term "gold-rush" is particularly appropriate to valuable specialty items such as abalone and lobsters, which initially allow the fisherman to make a large profit in a short time. This success can lead to growth of fishing power far beyond the biological potential of the resource, sometimes to levels at which almost no restrictions could be effective (FAO 1973). Gulland (1971) describes a commonly observed pattern in which the fishery develops faster than the biology can be assessed, and management actions are delayed because of sparse data.

In the early history of *H. kamtschatkana*, managers tried to prevent further increases in landings and to reduce landings. This action was based on an intuitive idea that landings were much higher than the stock could support for long. The tools used were limited entry, limitations on effort per boat, and reduced seasons. These failed to reduce catches, which actually increased in the first year after implementation and remained stable the next year despite a 60% reduced season. This occurred because effort per licensed entrant increased dramatically in several ways. In 1977, five boats took 66% of the catch, thus many boats were fishing at low efficiency. Licensees who previously fished alone increased their fishing team to three, creating a net increase in the total number of divers. Most diving for *H. kamtschatkana* takes place in shallow water, so divers increased the number of hours dived per day. Licensees moved their licences to larger boats, which allowed them to spend more time fishing and access to more remote beds. The British Columbia abalone fishery clearly illustrates that, attractive as effort control may seem as a management option (Hancock 1979), effort is actually very difficult to control if fishery units are free to compete with each other (Pearse 1982; Harrison 1983; FAO 1983). Pearse (1982, p. 79) suggests: "... fishermen and vesselowners will try to expand their fishing power whenever they compete with each other for an unspecified share of the catch of a common property resource, even if the fleet's capacity is already excessive." Despite this, attempts to reduce harvest by limiting entry are still made, for instance in the California abalone fishery (Hardy et al. 1982).

Management actions taken early in the B.C. abalone fishery may even have exacerbated problems by causing effort to increase faster than it might otherwise have. Since entry to several Canadian fisheries had been limited by 1976, some fishermen expected entry to abalone fishing to be limited. This expectation (well founded) probably led to some purely speculative fishing in 1976. When entry was limited, nearly all previous participants were included, and they continued to fish to protect the transfer value of their licence. Shortened seasons and the resulting competition among licensees resulted in greatly increased effort instead of reduced effort. When enough information became available to set explicit catch limits, 75% of the stock had already been removed (Breen 1980).

How should new fisheries like this be handled? Two essential requirements are to prevent possibly excessive effort from damaging a limited stock, and to obtain from the initial fishery some information about the dynamics of the stock. Gulland (1972) describes a system of arbitrarily limiting a new fishery to a small area, allowing unlimited fishing but with good monitoring, then expanding to new areas with restrictions based on performance of the first area. If initial effort is already too high for the stock to support, only one part of the stock is damaged. From the use of such a system in this fishery, it seems probable that stocks would not have been reduced by 75% in 3 years.

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A Comparison of Alternative Harvest Tactics for Invertebrate Fisheries

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HILBORN, R. 1986. A comparison of alternative harvest tactics for invertebrate fisheries, p. 313–317. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

This paper considers the merits of different harvest tactics such as annual catch quotas, season lengths, and effort limitation in relation to the biology of invertebrates, uncertainty in the management process and the objective of fishery management. Analysis indicates that when year-class strength is highly variable, unpredictable and few age classes are fished, then effort limitation or season length should be preferred to annual catch quotas. Since many invertebrates display very large and uncertain variability in year class strength, annual catch quotas should be considered carefully before being implemented in invertebrate stocks. The conclusions also depend upon uncertainty in fishing effort and in vulnerability of stock to effort. The problems in implementation of different tactics are discussed in relation to cost and reliability. A framework for quantitative comparison of tactics for a specific fishery is described.

La présente communication traite des avantages de diverses mesures de gestion de la récolte, notamment les contingents de prise annuels, la durée des saisons de pêche et la limitation de l'effort de pêche en relation avec la biologie des invertébrés, les incertitudes du processus de gestion et les objectifs de la gestion des pêches. L'analyse montre que lorsque l'importance de la classe annuelle est fortement variable et imprévisible et que la pêche ne porte que sur quelques classes d'âge, la limitation de l'effort de pêche ou le raccourcissement de la saison de pêche seraient préférables à l'imposition de contingents annuels. L'importance des classes d'âge de bon nombre d'invertébrés étant très variable et difficile à prévoir, les contingents de prise annuels devraient faire l'objet d'un examen détaillé avant d'être appliqués à des stocks d'invertébrés. Les conclusions pouvant être tirées sont aussi fonction de l'incertitude de l'effort de pêche et de la vulnérabilité des stocks à cet effort. On trouvera aussi une discussion des problèmes relatifs à la mise en place de diverses approches dans le contexte des coûts et de la fiabilité et l'on donne un cadre permettant la comparaison quantitative de mesures visant une pêche particulière.

Introduction

The biology of harvested invertebrates is often quite different from that of the majority of fin-fishes, since invertebrates frequently possess very high reproductive output, large variation in year class strength, rapid growth, and complex spatial distribution. As a result of these biological differences, the stock assessment tools that have been developed for finfish stocks, such as virtual population analysis, production models, and stock recruitment analysis are frequently not appropriate for analysis of invertebrate populations. Invertebrates often show no relationship between spawning stock and recruitment, which may be due to high reproductive output or the presence of invulnerable individuals in unfished or unfishable areas. Maximization of yield per recruit is quite often an appropriate harvest strategy for invertebrates, but will often result in recruitment overfishing of finfish stocks.

Given the biological differences between finfish and invertebrates one wonders if management methods used should not be fundamentally different. There is a tendency to adopt methods used in finfish management to invertebrates. For instance, in Canada, annual catch quotas have been set for many invertebrate stocks despite almost total ignorance about the population dynamics of these species. If year class strength is highly variable and the majority of the catch comes from one year class, then an annual catch quota is a poor regulation because the quota is totally unrelated to stock size. However, to consider the merits of any form of regulation and how it relates to the biology of the species being managed, we must take a more careful look at the objectives of the fishery, the harvest strategy adopted, and the tactical tools used to implement this strategy. This paper is a preliminary overview of the problem. I will discuss different objectives and strategies, and see how the tactics used to implement the strategies should be matched to the biology of the species being managed.

Harvest Objectives, Strategies, and Tactics

Fishery managers have many different types of objectives; maximization of biological yield, economic profit, foreign exchange, or employment are all objectives of fishery managers in some fisheries. If our objective is clearly stated and the biological dynamics of the species known, we can calculate the optimal harvest strategy (see Walters 1975; Walters and Hilborn 1978; Clark 1976).

We can describe most harvest strategies as the relationship between the catch and the stock size. Three types of harvest strategies are constant harvest rate, fixed escapement and constant catch (Doubleday 1976; Ludwig 1980). Figure 1 shows the relationship between catch and stock size for these three strategies; Figure 2 shows the harvest rate versus stock size for the same strategies. Obviously, infinite catch versus stock size strategies are possible, but I use these three as bench marks since they represent three possible extremes.

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The main types of harvesting strategies that do not map into such a graph are pulse harvesting where the catch depends upon time since last harvest as well as stock size, and probing strategies, which depend upon stock size and the uncertainty about stock production parameters.

Fixed harvest rate strategies are generally optimal when yield per recruit is to be maximized or when the total value of the catch does not increase linearly with the volume of the catch. Fixed escapement strategies are optimal when the average catch or economic yield is to be maximized, there is an important stock-recruitment curve, and stock dynamics are well known. A constant catch strategy would be optimal when minimization of year-to-year variability in catch is paramount. For invertebrate fisheries, where recruitment overfishing is frequently not a concern, a constant harvest strategy would most likely be optimal, but naturally the local biological, economic, and social concerns would have to be considered.

Once the harvest strategy is determined, we need to find the appropriate tactical tools to implement it. The most common tactics used in invertebrate fisheries are gear restrictions, vessel entry limitations, season lengths and annual catch quotas. These tactics can be simplified into three basic groups, those that regulate the amount of fishing time (seasons), those that regulate the catch to be allowed (quotas), and those that regulate the amount of effort to be expended (trip limits, vessel entry limitation). Gear restriction, which can include a minimum size limit, can be found in nearly every fishery in the world and they modify the harvest capacity of each vessel; therefore I have not included gear restrictions as a type of harvesting tactic.

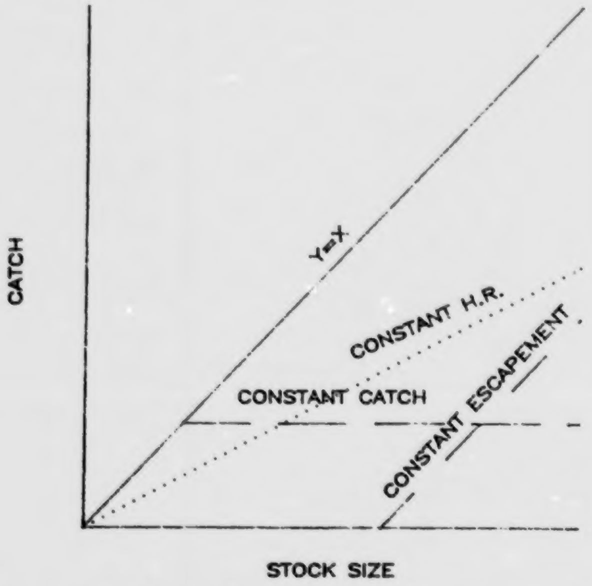

FIG. 1. The relationship between stock size and catch for fixed escapement, constant harvest rate, and constant catch quota harvesting strategies.

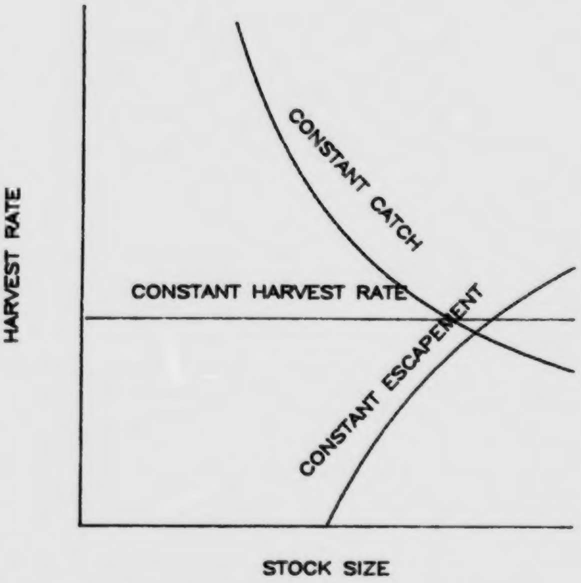

FIG. 2. The relationship between stock size and harvest rate for fixed escapement, constant harvest rate, and constant catch quota harvesting strategies.

If vessel entry is completely controlled, or if the harvest takes place in a very short period of time in which other boats could not respond to changing abundance, then season length and effort limitation might be equivalent. However, in most fisheries, even when the number of vessels is strictly limited, the vessels can vary the amount of fishing they do, so that season lengths are not equivalent to effort control.

To examine the relationship between harvest tactics and the desired harvesting strategy, we must look at the sequence of events involved in the fishery. At the beginning of a fishing season the manager is working with an estimate of stock abundance, an estimate of expected fishing effort, an estimate of the vulnerability of stock to gear, and a desired harvesting strategy. If stock size, effort, and vulnerability were known perfectly, then an annual catch quota, season length, or effort limit could all be used to achieve the desired catch and thus meet the requirements of the harvesting strategy perfectly. However, if stock size is not perfectly known, then the harvest will not be exactly as planned, and we may underharvest or overharvest the stock. Figure 3 shows the harvest rate achieved when it depends upon actual stock size. Catch quotas will cause the harvest rate to be higher than desired if the stock is lower than expected, and lower than desired if the stock is larger than expected. By using constant effort, we would expect the harvest rate achieved to be reasonably independent of stock size, although this does depend to some extent on the functional response of fishermen to stock abundance and is discussed in

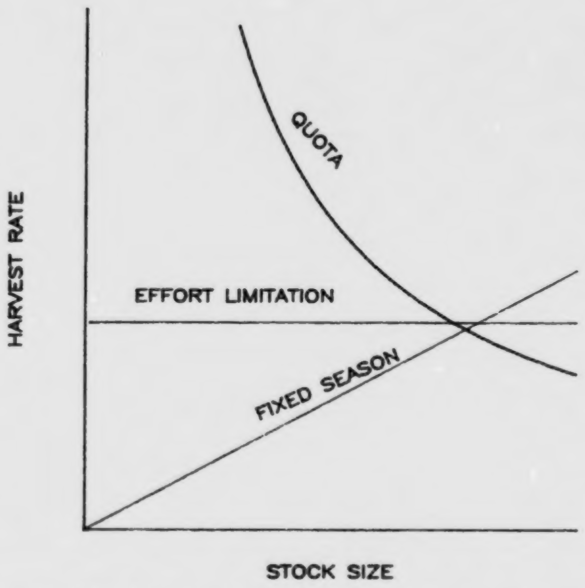

FIG. 3. The relationship between stock size and harvest rate for annual catch quota, fixed effort, and fixed season length harvesting tactics.

more detail in a later section. Using fixed season length we would expect the harvest rate to rise with stock abundance if effort can be increased by either fishing more when fishing is good, or by the entry of fishermen from outside areas. This phenomenon is known as the numerical response of fishermen and is also discussed in a later section.

Comparison of Fig. 2 and 3 shows some interesting results. Catch quotas are obviously preferred if a constant catch strategy is desired. Similarly, given a fixed escapement strategy, a season length appears to be most suitable and for a constant harvest rate strategy, a constant effort tactic seems best. All of the above comparisons are based on the assumption that stock abundance is the only uncertain variable. Table 1 summarizes the general relationship between strategy and tactics when the only uncertainty is stock size.

Unfortunately, we are often uncertain about vulnerability and expected effort as well as stock size. If stock size were known perfectly, then a catch quota would be a better tactic than either effort or season length limits no matter which strategy we wished to follow.

Table 2 summarizes the effects of uncertainty in stock size, vulnerability, and effort upon the various harvest tactics.

The above analysis indicates that if we accept a maximization of yield per recruit (constant harvest strategy) and believe that the dominant uncertainty is in stock abundance, then fixed effort emerges as the preferred tactic for invertebrates whereas an annual catch quota would be worst. However, this is such an oversimplification of the biology of invertebrates and harvest objectives that it would be misleading to leave the analysis at this level. Uncertainty also exists in vulnerability and in effort response, and all invertebrate fisheries are not characterized by one or two highly variable year-classes being fished. In the next sections of this paper I will discuss some of the other issues associated with the choice of harvest tactics and then lay out a quantitative framework for the rigorous analysis of specific situations.

TABLE 1. Strategy/tactic matches given uncertainty in stock size.

Strategy	Tactic		
	T.A.C.	Time	Effort
Escapement	worst	best	medium
Harvest rate	worst	medium	best
Quota	best	worst	medium

Implementation

Different harvest tactics have quite different implementation requirements and costs, as well as being distinguished by major differences in intrinsic reliability. Annual catch quotas require the most information and are the most expensive. Normally, the total landings to date are measured by multiplying the average catch per landing times the total number of landings. An estimate is also made of the number of vessels currently fishing and the amount they would have on board. Once the current landings plus the estimated amount on board vessels at sea is equal to the catch quota, the fishery is closed. Errors in the reliability of catch quotas can arise from each of the elements in the chain. Average landings may be misreported or not representative, estimates of the total number of landings can be in error for a number of reasons, and the vessels currently fishing may be making better or worse catches than those vessels already landed. When many vessels are involved or many ports are landing the catch, implementation of an annual catch quota can be very expensive.

Effort limitation requires the same effort measurement as does annual catch quotas, but does not require landings per vessel, so is intrinsically less expensive and more reliable than annual catch quotas. Season length is by far the most reliable tactic since management consists of simply guaranteeing that no one is fishing out of season. This probably accounts for its widespread use in many of the world's fisheries.

Functional and Numerical Response

When season length or effort limitation are used, the actual catch will depend upon the abundance of the stock and how the fishing vessels respond to this abundance. Figure 3 represents the simplest assumptions about the response of fishing vessels. There is much theory associated with predators' (fishermen for instance) response to the abundance of their prey.

The relationship between prey abundance and number of prey captured per predator is normally referred to as the predators' functional response (Holling 1959) in the ecological literature. The simplest model, often used in fisheries, is that catch per fisherman (predator) is proportional to abundance of prey. This means that the harvest rate is proportional to effort and based on the assumption of random encounters between prey

TABLE 2.

Effect of Uncertainty in:	Effect of Uncertainty on: T.A.C.	Time	Effort
Stock size	low stock high harvest	lower stock lower harvest rate	constant harvest rate
Vulnerability	none	higher vulnerability higher harvest rate	higher vulnerability higher harvest rate
Effort	none	higher effort higher harvest rate	none

and the fishing vessels, without any time consumed in capture, handling, or travel to and from port. Once we include these time components into the time budget of the fishermen, however, the growth in catch starts to slow down as stock abundance increases, because vessels spend more and more time capturing, handling, and returning to port.

The ecological term used when fishermen modify their fishing effort in relation to abundance is the numerical response of predators to prey abundance (Soloman 1949). This numerical response will alter the harvest rate achieved during any season length. There are likely to be two major causes of numerical response, economics of vessel operation and alternative fishing opportunities. A single fleet with no alternative fishing stocks or locations would probably show lower effort when stock abundance is low simply because the catch per unit of fishing effort would no longer be economical for some operators. In fact at zero abundance we would expect the effort to be only exploratory. As soon as it was determined that there are no fish, no one would go fishing. As abundance increases, there should be more fishing effort as fishing becomes profitable for more fishermen. At very high abundance we might see a drop in effort as fishermen trade free time for additional catch.

When there are alternative fishing opportunities there should be an even stronger numerical response to abundance. At low abundance most fishermen will fish elsewhere, but at high abundance most fishermen will concentrate on the abundant stock. The numerical response will cause harvest rates to be higher when stocks are abundant and lower when stocks are scarce. This is the ideal type of change for a fixed escapement strategy but most unwelcome under a strategy of constant catch.

Consequences of Error

To evaluate the merits of different management tactics we need to be able to measure what is lost by not achieving the target catch for the particular strategy. When using a fixed escapement strategy with a tactic of annual catch quotas, what do we lose by under or over escapement?

We need to go one step back from our strategy to see how our objective is compromised by imprecision due to tactical tools. Fixed escapement is the easiest strategy to analyze because it is the optimum strategy when the objective is maximization of long term average catch with known stock dynamics. Thus we can ask how much is lost in long term average catch using different tactics.

The consequences of underescapement are reduction of future recruitment by reducing the spawning stock and reduction of future yield by harvesting the stock too young with a subsequent loss of growth. The consequences of overescapement are the loss of potential catch and the potential loss of recruitment if larger stock sizes produce smaller year classes. This loss of recruitment occurs only when the stock recruitment relationship bends over on the right hand side. The natural mortality rate will have a significant effect on the cost of overescapement. If there is low natural mortality, the catch missed this year can be caught next year and little is lost. However, if natural mortality is high (often the case with invertebrates), the catch foregone this year is lost.

If we believe that our harvesting does not affect recruitment, as is often a stated or unstated assumption in invertebrate fisheries, then the costs of under and overfishing can be analyzed reasonably directly in yield-per-recruit analysis. High natural mortality rates and very rapid growth rates will both make the cost of over and underharvesting higher because mistakes cannot be corrected in subsequent seasons.

Discussion

We have considered the tradeoffs between the costs of implementation, the uncertainty in stock size, vulnerability and effort, and the actual management objective. Any analysis of alternative harvest tactics should consider all these factors. We can make a few generalizations as in Table 1, but these are so general as to serve only as a rough guide. Even Table 1 does not explicitly consider the management objective. Therefore, rather than providing a set of firm answers, I have only been able to raise the major issues. For any specific fishery, alternative tactics can be quantitatively evaluated by building a simulation model of the stock dynamics and the management process similar to that of Hilborn (1979). Stock dynamics and natural variation in stock dynamics need to be included as well as harvest regulation dynamics and errors in implementation of catch quotas, season lengths, and effort limitation. Hilborn (1979) did not include errors in the implementation tactics.

Only by including the uncertainties in each element of the biology and management can we properly evaluate the trade-offs between different tactics. To my knowledge this has not been done in any invertebrate fishery.

A second useful step would be to review the major uncertainties in invertebrate fisheries. I have described invertebrates as having large year-to-year variation in year-class strength, relatively weak stock recruitment curves, and complex spatial distributions. I have been unable to find enough data on year-class strengths in invertebrates to compare them to those of finfish, nor can I quantitatively demonstrate that invertebrate stock recruitment relationships are much weaker than finfish. It would be most valuable for someone familiar with many invertebrate stocks to summarize important life history parameters in a form comparable to exploited stocks of other taxa.

Acknowledgements

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Generalizations and Recent Usages of Yield Per Recruit Analysis

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Yield per recruit analysis optimizes yield for a cohort by balancing growth and mortality. It enjoys widespread use because of its modest data requirements and ease of interpretation. Traditionally used methods are reviewed. The technique has been generalized to include cases of non-stable age distribution, inclusion of recruitment information, and abundance-dependent behavior in the fishery. We conclude that a form of stock projection is the most versatile form of yield per recruit analysis.

L'analyse du rendement par recrue optimise le rendement pour une cohorte par l'équilibrage de la croissance et de la mortalité. Cette méthode connaît une grande popularité en raison de ses modestes exigences en données et sa facilité d'interprétation. L'auteur passe en revue les méthodes traditionnelles à employer. La technique a été généralisée de manière à englober des cas de distribution d'âge non stable, des informations sur le recrutement ainsi que le comportement dépendant de l'abondance dans la pêcherie. L'auteur en vient à la conclusion qu'une forme de projection des stocks constitue la forme la plus polyvalente d'analyse du rendement par recrue.

Introduction

Yield per recruit analysis is the name given to a number of related methods that attempt to optimize yield from a cohort over a range of fishing mortality patterns and intensities. The method is popular because of its relative simplicity, which is manifest in modest data and computational requirements and ease of interpretation. Required data are growth and mortality as a function of age. Mortality is partitioned into natural and fishing mortalities. The latter mortality results in catch or yield, and natural mortality is an aggregation of all other sources of removal. The simplicity of the yield per recruit approach may mean that it represents an oversimplification and is not applicable to a real fishery. It also is weakened in that it produces a relative index, that is per recruit; and such information may be of limited utility.

We proceed by reviewing the management modelling process, then the yield per recruit model itself. Three extensions to commonly used analyses are then presented. The first is a decomposition of contributions to the total yield from a cohort. The second is a means of relating yield per recruit and stock-recruit information; and third, analysis is generalized to include an element of behavior of a fishing fleet, which is the ability of a fisherman to direct his effort onto a specific size distribution in the catch. Unfortunately, inclusion of fishing behavior renders the problem insoluble except by iteration, and generally requires a computer simulation of yield. Because topics covered in this paper are more or less discrete subjects within the realm of yield per recruit analysis, each topic will be presented and developed individually and then an overall summary and discussion will follow. Examples used to aid in describing the various methods are from the Georges Bank sea scallop (*Placopecten magellanicus*) fishery except where noted otherwise.

Reliability of the management system is seen to be dependent on the ability to forecast accurately (Rosen 1974). This is of particular interest in the case of advice based on a yield per recruit model. A number of recruits is assumed to enter the fishery at a given age. Over the first year, or any other convenient period, recruits will grow and a certain fraction will die, of which a portion will be harvested and represent yield. The fraction that survive will go through the same process the following year. Total yield from this cohort is found by summing contributions from each period as one follows the cohort. However, fishing policy is not set along cohorts but rather for a given year. The ability to substitute the cohort's performance for standing stock in a year is called a principle of equivalence by Sinclair et al. (1983). The system must be sufficiently stable into the near future to allow a projection, with a second requirement that if stable the results can be applied to a standing stock, i.e. equivalence instead of recruitment. We will consider these points in more detail in the discussion below.

Description of Yield Per Recruit Analysis

In this section formulae for determination of yield per recruit (*Y/R*) will be reviewed and developed. This section emphasizes the descriptive phase of the process. The basis for yield per recruit is the balancing of growth and death or equivalently balancing survivors and removals. Survivorship from one period, *t*, to the next is simply described by modelling removals as proportional to numbers present.

(1) $N_{a+1,\,t+1} = N_{a,t}e^{-Z_{a,t}}$

(2) $C_a = F_a\bar{N}_a$

where $N_{a,t}$ is the number of animals of age a in period t and $Z(a,t)$ is total mortality as a function of time and age which is comprised of natural $M(a,t)$ and fishing $F(a,t)$ components. Often, and generally hereafter, time is explicitly removed from Equation 1 as the time interval is assumed to be a unit period. Also, we do not need the generality of both age and time arguments so that natural mortality is assumed to be a constant over both age and time and for present fishing mortality is assumed to be only a function of age. The catch over one period is described by Baranov's (1918) catch equation.

(3) $\bar{N}_a = \dfrac{1-e^{-Z_a}}{Z_a} N_a$

The bar over N (and later over B) signifies the average over a period. Catch in numbers at age as well as the standing stock in numbers at age can be converted to yield and biomass respectively by appropriate weights, which for convenience will be assumed to be a function of age only.

(4) $Y_a = W_aC_a = F_a\bar{B}_a$

where

(5) $\bar{B}_a = W_a\bar{N}_a$

If growth rate, G_a, is modelled as the logarithmic difference of weight at age,

(6) $G_a = \ell n\,(W_{a+1}/W_a)$

(7) $B_{a+1} = B_a e^{G_a - M_a - F_a}$

Natural parameters, growth and mortality, are measured or inferred and then for any age-dependent fishing mortality, catch, yield, and standing stock size can be estimated or forecast. Shape of the yield curve defines target F levels. The F value which gives the highest yield is called F_{max} (Fig. 1). while the more conservative $F_{0.1}$ (Gulland and Boerema 1973) is defined as the value of F which has a catch rate one-tenth of the theoretical rate for a virgin fishery. The four most commonly used formulations of yield per recruit are attributed to Baranov (1918), Thompson and Bell (1934), Ricker (1945), and Beverton and Holt (1957). These methods have been reviewed elsewhere and anyone interested in details of the calculation is referred to Ricker (1975). The principle discriminating characteristics among these methods is the manner in which growth is modelled.

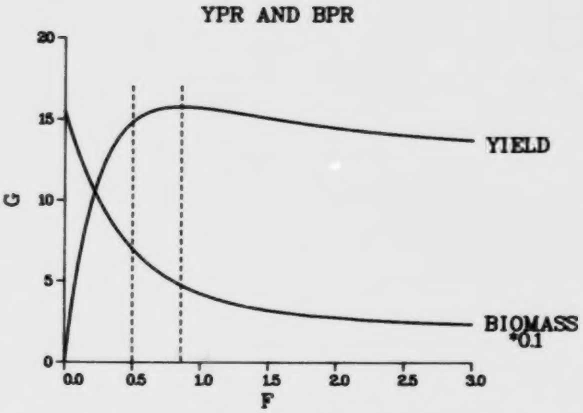

FIG. 1. Yield per recruit and biomass per recruit for the Georges Bank scallop stock. The dashed line on the right marks F_{max} and the one on the left, $F_{0.1}$.

Baranov's method differs from the others in that summation down the cohort is done over lengths not ages. Thus, growth is in terms of weight at length, not age. This means that mortality must also be a function of length or a relationship be established to relate length and time. Baranov relates length and time by assuming that length is a linear function over the recruited ages of the fish. An isometric (weight at age proportional to length cubed) length-weight relationship is further assumed. Summation over the cohort can now be done directly to give average number of animals alive from each age (length) class in the cohort as well as biomass. If a fishing mortality is assumed that is constant for all age classes yield can also be found analytically. This method suffers from the restrictive length-age and length-weight assumptions as well as constraints imposed by assuming constant natural and fishing mortalities for all animals in recruited ages.

Thompson and Bell (1934) incorporate weight at age directly instead of assuming a growth model. This is done by determining weights at age averaged over each period of the recruited population. These weights are multiplied by numbers at age as determined from Equation 1 to give biomass at ages for any assumed pattern of fishing mortality. This is probably the simplest method to employ and is not constrained by a specific growth model. Natural and fishing mortality may be functions of age.

Ricker's (1945) method is closely related to Thompson's and Bell's. The principle difference is that instead of using average weights for each period weights at each age entering each period are converted into growth rates by Equation 6. This method allows one to determine average weight over the period as the simple mean of the endpoint weights or to integrate over the period to determine a mean value weighted by numbers at age. Its other assumptions and constraints are as for Thompson's and Bell's.

The method ascribed to Beverton and Holt (1957) is based on the von Bertalanffy length at age relationship (Ricker 1975) and an isometric length-weight relationship. Growth data are first fit to this equation to determine appropriate parameters. Then, as for Baranov's method, the yield and standing stock for the cohort can be expressed analytically, although this method has the advantage of a more realistic growth function. An extension of this approach for crustacea was presented by Caddy (1977) in which the growth function was expressed in terms of molt increment and frequency.

Yield Decomposition

If we recall Equations 4 and 7, yield and surviving biomass may be described as functions of two natural phenomena, growth and natural mortality, and a man-induced effect, fishing mortality. Strategies are compared by assessing predicted yields after varying the intensity and pattern of fishing mortality. If fishing effort could be concentrated on only one age for a year after the cohort has grown and survived from the nominal age of recruitment, this would be equivalent to one contribution to a yield per recruit calculation. Alternatively, one may think of total yield in a yield per recruit calculation as contributions from separate fisheries — one for 3 yr olds, one for 4 yr olds, etc. Yield contribution for each age is written as a function of age, *a*, and fishing mortality, *F*, and is primed to distinguish it from our previous usage of yield.

$$(8) \quad Y = \sum_a V_a Y_a' (F_a)$$

$$Y_a' (F_a) = \frac{W_a F_a (1 - e^{-Z_a})}{Z_a} \prod_{i<a} e^{-M_i}$$

where the weighting factor V_a is composed of two parts. The first part is a factor to correct for divergences from stable age distribution, and the second is a correction for removals by fishing of ages younger than *a*.

$$(9) \quad V_a = R_a e^{-\sum_{i<a} F_i}$$

where R_a is the ratio of observed numbers at age (or standing stock) to stable distribution. Stable age distribution is proportional to accumulated effects of total fishing mortality. Correction for divergences from stable age distribution may be used to apply the model to cases where migration is a major consideration or to apply it to a standing stock which may not be a stable configuration. Summation of previous fishing is required to account for such removals. To evaluate R_a, we recall that the decomposed yield table incorporates growth and natural mortality information and that effects of fishing mortality are included explicitly in Equation 9. Any deviation from numbers at age predicted by these three factors and what is observed for the stock in question is accounted for by dividing observed values into predicted ones, and the resultant we define to be R_a. This constitutes a generalization of the recruitment concept. For example, if R_4 were 1.5 that means that 50% more 4 yr olds are seen in the stock than would be predicted and the surplus may be thought of as recruits through migration. Care must be exercised when using R_a's different from unity to ensure that a valid basis of comparison exists between strategies.

Table 1 contains the decomposed yield for the Georges Bank scallop stock as derived from Equation 8. Note that age of capture is the column heading while fishing mortality is varied over the rows. This reverses the axes from the usual practice for yield isopleths and was done to emphasize the relationship between decomposition, standard yield per recruit, and partial recruitment. We see that the column for capture at age 8 has the greatest values of any column. The top row, $F = 50$, approximates standing stock available at age. Higher fishing mortality means more of the age group is taken and fewer are available for subsequent capture. The second column, exponential of $-F$, is the fraction surviving fishing. If one wanted to reconstruct results for a given partial recruitment vector the contributions of successive ages are summed after weighting for survivorship after fishing (assuming here a stable age distribution). Explicitly, if paritial recruitment were 0.6, 1, and 0.8 for ages 3, 4, and 6, respectively, the yield per recruit would be:

$$\begin{aligned}(10) \quad Y &= V_3 Y_3'(0.6) + V_4 Y_4'(1) + V_6 Y_6'(0.8) \\ &= (1 \times 3.17) + (0.55 \times 8.23) + \\ &\quad (0.55 \times 0.37 \times 11.65) \\ &= 3.17 + 4.53 + 2.37 \\ &= 10.07\end{aligned}$$

Contributions from each age are evident.

TABLE 1. Yield contributions from a single age.

		Age (yr)							
F	e^{-F}	3	4	5	6	7	8	9	10+
50.0	0.00	7.34	13.55	18.71	22.03	23.58	23.82	23.20	22.05
2.0	0.14	6.14	11.34	15.67	18.45	19.75	19.95	19.42	21.05
1.8	0.17	5.92	10.94	15.11	17.79	19.04	19.23	18.73	20.93
1.6	0.20	5.65	10.44	14.42	16.98	18.18	18.36	17.88	20.80
1.4	0.25	5.33	9.84	13.59	16.01	17.13	17.31	16.85	20.62
1.2	0.30	4.94	9.11	12.59	14.82	15.87	16.03	15.61	20.40
1.0	0.37	4.46	8.23	11.37	13.39	14.33	14.47	14.10	20.09
0.8	0.45	3.88	7.16	9.89	11.65	12.46	12.59	12.26	19.64
0.6	0.55	3.17	5.86	8.09	9.53	10.20	10.30	10.03	18.94
0.4	0.67	2.31	4.27	5.90	6.95	7.44	7.51	7.32	17.68
0.2	0.82	1.27	2.35	3.24	3.81	4.08	4.12	4.02	14.73

Linkage of Yield Per Recruit and Stock-Recruit Relationships

Amalgamation of yield per recruit analysis and stock recruit information that follows is based on work initiated at an International Council for the Exploration of the Sea (ICES) ad hoc working group and reported in Anon. 1984. Objective of the study was to find alternative target exploitation levels to $F_{0.1}$ and F_{max}. Yield per recruit results are generally plotted as yield and biomass per recruit as a function of F (Fig. 2) while stock-recruit information is in the form of recruitment as a function of biomass. Slope of the line joining the origin to the mean of stock sizes and recruitments represents average recruitment per standing stock. This value is the reciprocal of biomass per recruit and by this the two relationships may be linked. Similarly, slopes representing good or poor recruitment (which may be approximated by the ninth and first deciles) can be defined and then related to an F level or via biomass per recruit, to the yield per recruit graph.

Combining these two relationships may be thought of as closing the life cycle. Biomass per recruit describes average growth and survivorship of a cohort, and the stock-recruit relationship takes the standing stock forward to a subsequent recruitment. Of course we have assumed stability over an appropriate period. The combination of these types of information may be thought of in the context of a generalized Leslie matrix. Stock-recruit information is contained in the first row of the Leslie matrix which describes fecundity as a function of age and perhaps biomass. Yield per recruit analysis is then an analog to the off-diagonal terms of the Leslie matrix which specifies removals at age. The difference is that they work in concert in the Leslie matrix but independently in the present context.

Stock-recruit relationships are fairly rare for marine invertebrate stocks as the requisite data are difficult and expensive to obtain and generally noisy. Simulated amorphous data as shown in Fig. 2, are unfortunately all too common in invertebrate research. Occasionally, however, better relationships are found. For example, Fogarty (1983) defined a stock-recruit curve which fit lobster data well. In such a case (Fig. 3) lines, actually secants, may be determined to define good and poor recruitments which may be linked via biomass per recruit to a F level.

Recently, Getz and Swartzman (1981) described a method of presenting stock-recruit data which is intermediate between the amorphous data and a well-fit functional relationship. Figure 4 contains scallop data which would not fit a curve well nor are completely without structure. The data are derived from the Georges Bank Subarea 5Ze scallop stock, and in this case two stock size regions and three recruitment regions have been defined. A portion (o) of the stock and recruitment data is from a cohort analysis (Mohn et al. 1984) and the remainder (+) is from regressions of recruitment and stock size on catch which allows extension of the data 11 yr outside the range of cohort analysis. This was possible as recruitment and subsequent catch of 5 yr olds was significantly correlated.

It could be described as having a trend of negative density-dependence with a few good recruitments at higher parent biomass. Such data may be arbitrarily partitioned in both dimensions. For each standing stock division the recruitment may be either good, medium, or poor with probabilities derived from the data or assumptions. A simple approach to estimate such probabilities would be to set them proportional to the number of occurrences in each recruitment class. Thus, for high biomass levels one would expect poor recruitment half (three-sixths) of the time. Of course more sophisticated methods may be employed to estimate probabilities of recruitment level from a given standing stock level. Also, the independent axis need not be standing stock but may be any index of reproductive potential of a population. Once stock and recruitment cell sizes have been determined a mean may be found for each cell and a slope determined from the origin to the cell mean. The position along the y-axis of the mean of each cell is the stock contribution, and spread in the y-direction reflects the magnitude of environmental and biological influences. Thus, for an estimated stock size the F levels for good or poor recruitment may be found on the Y/R plot. The Y/R plot shows the conventional $F_{0.1}$ and F_{max} levels as well as those defined from inclu-

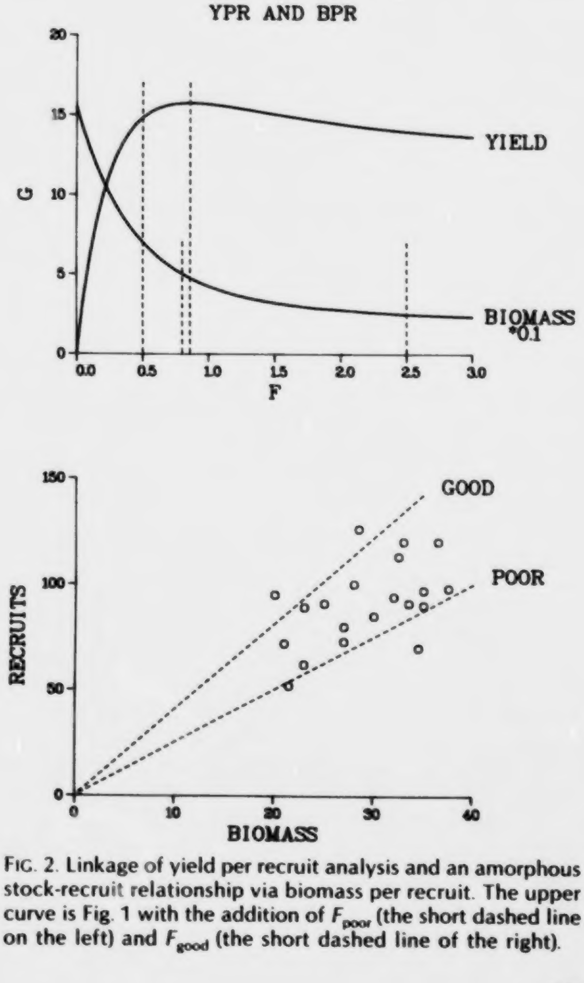

FIG. 2. Linkage of yield per recruit analysis and an amorphous stock-recruit relationship via biomass per recruit. The upper curve is Fig. 1 with the addition of F_{poor} (the short dashed line on the left) and F_{good} (the short dashed line of the right).

sion of recruitment information for a poor parent biomass, the present situation. Inclusion of recruitment gives F levels on either side of $F_{0.1}$, with higher likelihood for lower values based on the higher frequency of medium recruitment from poor parent biomass.

Stock Projection and Yield Per Recruit

As was mentioned above, Y/R analysis is usually combined with a catch projection by multiplying the F level by the selectivity and estimated standing stock biomass. The process could be reversed, however, by taking the estimated standing stock and projecting it via Equation 1 at various F levels to find a series of Y's. An optimal yield as defined by a maximum, 0.1, or other criteria could then be selected from the runs and the F that produced it noted. Information required is the same as for a Y/R analysis, namely growth, mortality, and an assumed fishing strategy. If a constant recruitment is assumed the stock can be projected ahead until the yield is stable, and optimal F's will be identical to results of Y/R analysis. Stock forecasts are generally carried out on a computer and require more calculations than the analogous Y/R determination. This process is known as stock projection and is commonly used to assess the short-term impact of a catch or effort limitation and to estimate a total allowable catch from a target F level (Beverton and Holt 1957; Walters 1969). Moreover, the technique is easily generalized to allow inclusion of stock-recruit information or more complex behavior of the fishing fleet. If instead of constant recruitment, a recruitment function were incorporated into the stock projection program, results from various harvesting strategies could be compared. Comparison would give the best harvesting strategy for a given stock-recruit relationship instead of the best strategy per recruit. An example of this is shown in Fig. 5 for the Georges Bank sea scallop stock, assuming, in spite of the evidence in Fig. 4, that scallop recruitment may be adequately described by a Ricker (1975) recruitment function with parameters $a = 0.06$ and $b = 0.001$ (Fig. 3). When compared to the Y/R which is replotted from Fig. 3, it is seen that the stock is less robust to heavy exploitation when the recruitment function is included in the analysis. This would be expected from the domed shape of the Ricker curve.

Stock projection may also be used to generalize Y/R with regards to harvesting. In the case of Georges Bank scallops selectivity of the gear does not determine size distribution of the catch. This is true in many invertebrate and finfish fisheries when stock is size-aggregated and its spatial distribution is sufficiently stable that a patch may be exploited. In the case of scallops the fleet directs its efforts to capture 4, 5, and 6 yr old animals. Partial reasons for this are that younger animals require too much labour to shuck, older animals are sparsely distributed, and market considerations. Fishing mortality over time and age is most commonly described as though it were the product of three independent factors,

$$(11) \quad F_{a,t} = qS_aE_t$$

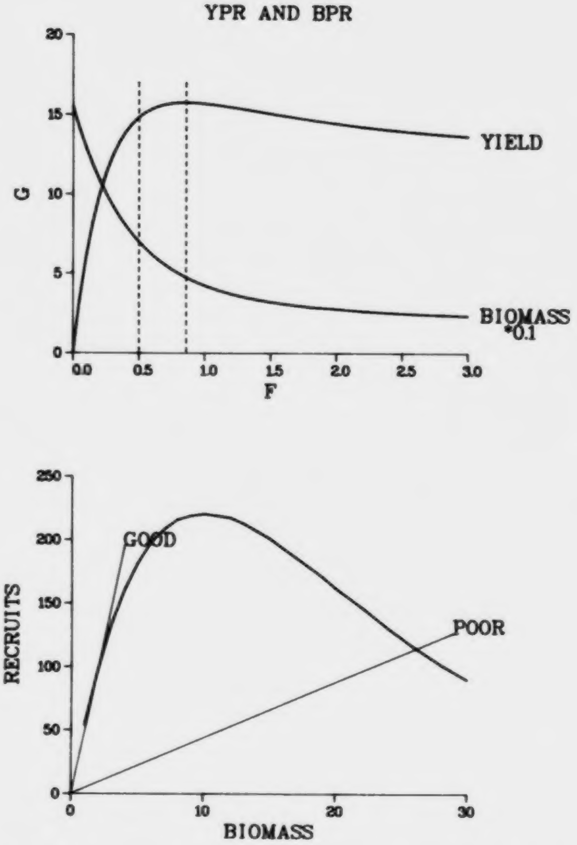

FIG. 3. Linkage of yield per recruit analysis and an assumed functional Ricker stock-recruit relationship ($a = 0.06$, $b = 0.001$) via biomass per recruit F_{poor} and F_{good} are not shown in the upper figure because the former is essentially zero and the latter is off scale to the right.

where q is the catchability, $S(a)$ the selectivity, and $E(t)$ the effort pattern from year to year (Doubleday 1976; Pope and Shepherd 1982). Also by convention, selectivity is normalized such that its largest element is of unit magnitude. To expand this definition of fishing mortality to include behavior of the fishing fleet in response to distribution of the biomass over ages fished, a fourth component to the above definition is added, which I call the behavioral parameter (β_a):

$$(12) \quad F_{a,t} = qS_a \, \beta_aE_t$$

Although β_a was defined as a function of abundance at age it could be expanded to include other factors which influence distribution of fishing effort such as preferred prices for certain size animals or protection of spawning animals. In order not to redefine the familiar quantities $qS(a)$ and $E(t)$, it is proposed that the behavioral parameter be normalized to have unit area ($\sum_a \beta_a = 1$) if it is an age vector or unit volume if the effort and behavior are changing in time within a data period (i.e. year in our context).

The stimulus for introducing the behavioral parameter is the practice of "blending" scallop meats to attain

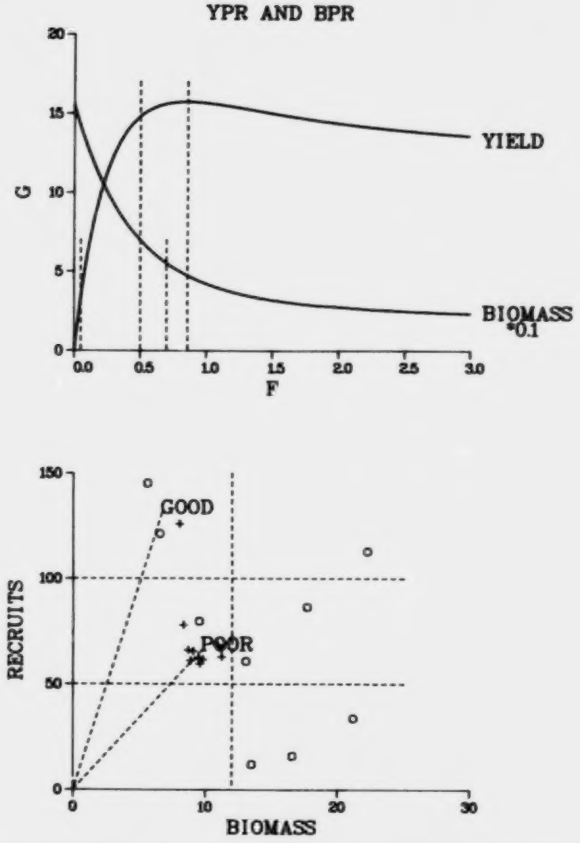

FIG. 4. Linkage of yield per recruit analysis and an intermediate stock-recruit (Georges Bank scallops) relationship via biomass per recruit. With a low parent biomass F_{poor} is the short dashed line of the left and F_{good} is the short dashed line on the right. Lines marked 'GOOD' and 'POOR' on the lower plot are drawn from the origin to the center of observations for each cell.

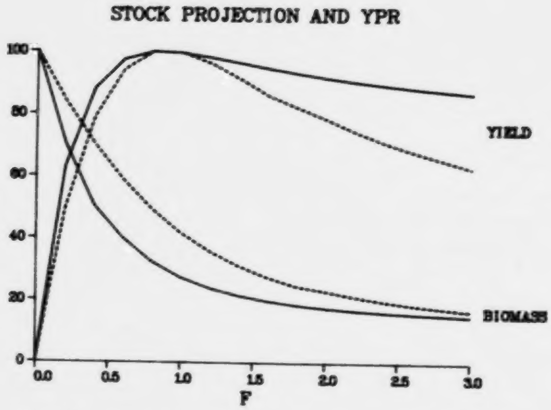

FIG. 5. Relative yield and biomass per recruit from Thompson–Bell (solid) and stock projection (dashed) including the Ricker stock recruit function from Fig. 3. The Y-axis has been normalized to allow the comparison of yield per recruit and yield.

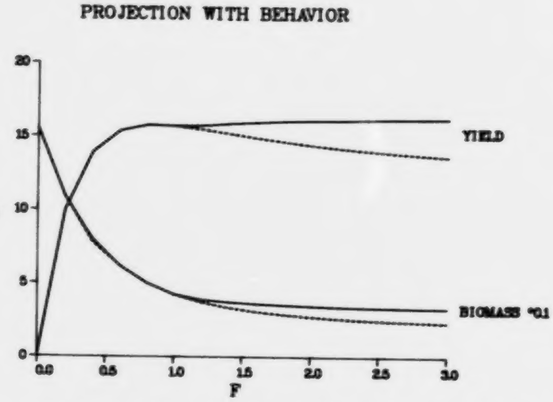

FIG. 6. Yield and biomass per recruit from Thompson-Bell (solid) and stock projection (dashed) including behavior in terms of a blending strategy.

a stipulated minimum average weight. At writing, maximum legal meat counts for Canadian scallops on Georges Bank is 77 per kg (35 per pound). Fishermen may choose to capture a large number of small animals, which generally occur in dense concentrations, and blend them with a small number of large ones to reach their target average. Of course, if small animals are so abundant that sufficient large animals are not available, then effort must be reduced on smaller animals. Thus it is seen that abundance at age modifies distribution of effort. No method of *Y/R* known to the author would be applicable to this situation. Therefore, a stock projection simulation which can iteratively check mean size of the catch and modify effort via the behavioral parameter was written. This type of projection could also be used to compare management strategies when the fleet follows a strong year class, as is a common practice, by appropriately redefining β.

Results of a projection are shown in Fig. 6 which shows the use of a stock projection to obtain a *Y/R* under a blending strategy. The behavioral parameter which is used displaces effort from animals under the target average to those over the average in such a way that total mortality is unchanged. For simplicity, intensity is reduced by one factor for all animals under the limit and increased by a second factor for all animals over. Thus, effort directed against 2, 3, and 4 yr olds may be reduced by 20% and against 5+ yr olds increased by 6% in order to reach a specific average catch weight with a given selectivity and stock size composition. The target weight for blending is a 20 g meat. This value was chosen as it causes the blending to become restrictive at fishing levels just above those now seen on Georges Bank. β_a is initially defined to be uniform for all ages and a catch is determined from the standing stock, qS_a and effort. Mean weight of the catch is compared to target level, and if the weight is too low, those β_a's above the target weight are increased and those beneath decreased to simulate a transferal of effort. This process is repeated until target catch weight is achieved. Figure 6 shows yield and biomass per recruit as a function of increasing effort for a blending strategy. Blending is seen to be more stable with high fishing mortality than the reference *Y/R* result which assumes a fixed fishing pattern. There is no formal reason prohibiting the further generalization of this approach to include both stock-recruit and the behavioral parameter.

Discussion

The management process incorporates ideas of the descriptive and predictive roles in modelling. First, the stock must be adequately described; then, predictions are based on the description. Yield per recruit analysis was seen to embody the predictive role in determination of growth and natural mortality of the stock. The predictive role used this description in conjunction with trial fishing strategies to predict yields. Yields were then optimized with respect to a goal or objective, maximum or 0.1 yields being the most common, in order to find the best fishing pattern and intensity. If a TAC were required a further prediction could be made by applying the optimal *F* to the estimated standing stock. Inherent in both these predictions is the idea that conditions which prevailed when natural parameters were estimated will still be appropriate over the period of prediction. Stability of description should not be confused with population stability. A stock could collapse due to overfishing. If the growth, natural mortality, and fishing pattern had been adequately described and did not change during the collapse then the description was stable while the stock was not; and the collapse would have been predictable. A further distinction is important; descriptive stability does not prohibit such effects as density-dependent growth or changes in fishing patterns, only that these effects can be described for a sufficiently long duration.

A central idea in yield per recruit analysis, and indeed many management strategies, may be stated as "take some now and leave some to grow for later." This is done in *Y/R* on a cohort basis, but stocks are not generally managed by cohort but on an annual basis for the entire recruited population. If one could keep the same policy in place for a long period of time a sufficient number of cohorts would be included in the management strategy to approximate the recruited stock. In other words, if a strong cohort enters the fishery the *F* levels determined for the stable age distribution would be too high while the cohort is beneath the age of maximum biomass and too low when it is over; but over a sufficiently long period these two errors will tend to cancel. Sinclair et al. (1983) give some specific examples of this problem. Unfortunately, what is often required is the catch level for the upcoming year, not the upcoming decade, and *Y/R* cannot be used directly to assess the situation. On a 1 yr basis, optimizing yield means take all the resource possible. What is required is a more comprehensive objective than yield alone which would assure sufficient stock for both short-term growth and long-term recruitment. Neither *Y/R* nor extensions reported in this study can answer the problem of what to do for the short term. Solution of this question requires techniques of mathematical programming and game theory which represent a level of sophistication beyond the present context.

The first extension to *Y/R* presented was called yield decomposition which allows determination and manipulation of individual age contributions to total yield per recruit. Results of the decomposition are presented in a tabular form which is then reassembled with fishing pressure and selectivity. In terms of numbers of calculations required it is more efficient to proceed this way, if a large number of different selectivities are to be tried, than by the usual Thompson-Bell method. Also the decomposed representation offers some insights into migrating stocks and non-equilibrium stock distributions.

The second extension of *Y/R* was to link it to a stock recruit relationship in order to define target F levels that take into account the reproductive potential of the stock. Target *F* levels, F_{good} and F_{poor}, are set from the biomass per recruit curve as opposed to F_{max} and $F_{0.1}$ which are defined from the yield per recruit curve. Results are still presented on a per recruit basis even though sufficient information exists to give yields in terms of biomass. Information required and the method in which it is used in this approach is closely related to the Leslie matrix. There is some internal inconsistency with this approach in that *Y/R* purposely removes effects of variable recruitment while the stock-recruit relationship is based on determining causes of such variation. Nevertheless, the method seems quite robust and has been seen to work with stock-recruit data that range from a well fit functional form to an amorphous collection of points. However, with the Ricker recruitment model biomass per recruit produces such a wide range between F_{good} and F_{poor} that results tend to be useless.

Stock projection has been defined as a stock simulation based on removals proportional to abundance via both natural and fishing mortalities. It can be used for short-term projections from a non-equilibrium stock or for longer term projections to determine optimal strategies of removal. It can reproduce results of all the other types of *Y/R* analysis discussed here and may be expanded to directly incorporate stock-recruit and fishing fleet behavioral information. It also benefits from a clear distinction between the descriptive and predictive roles of management modelling. This is contrasted to traditional *Y/R* which has the problem of being defined for a cohort but being applied to a standing stock. The yield per recruit and stock recruit information from the assumed Ricker model have been coordinated in two manners. First, coordination was done via biomass per recruit (Fig. 3), and in this case the target *F* levels were of no practical value due to their extreme values (nearly zero and above 3). Second, they were coordinated by incorporating the stock-recruit curve into the stock projection. Although only 16 points were used (Fig. 5) F_{max} was not affected and $F_{0.1}$ only shifted to the right slightly. Of more importance is the shape of the yield curve as *F* is increased beyond F_{max}. Yield is less stable to overexploitation than would be predicted from the strict yield per recruit approach.

It is seen that both standard *Y/R* models and stock projections require the same basic biological data, growth and mortality rates or their equivalents. The former group is constrained to stable age distributions and equilibrium conditions. On the other hand, stock projections are essentially dynamic. However, they may be run for sufficiently long periods to reach equilibrium. If this is done, the output, as well as input, would be equivalent to *Y/R* models. Therefore, in a functional sense, stock projections which have been run to equilibrium may be thought of as *Y/R* models.

All methods that we have discussed are based on a partitioning of removals into catch and loss through natural mortality. Strategies are compared on the bases of yield per recruit and in some cases biomass per recruit. Assumptions required are less restrictive than the class of popular management models known as surplus production. Surplus production models incorporate assumptions of density-dependent growth, carrying capacity, and in many cases assume the fishery is in equilibrium. With the wider usage and acceptance of computer simulation, yield per recruit analysis in its most powerful form, stock projection, should become increasingly popular.

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Management of Dungeness Crab Fisheries

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METHOT, R. D., JR. 1986. Management of Dungeness crab fisheries, p. 326–334. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92

Management of Dungeness crab fisheries in the states of California, Oregon, and Washington was reviewed by the Pacific Fishery Management Council in 1979 and may be considered in three categories: conservation of the resource, maintenance of product quality, and reduction of conflicts. Size limits and prohibition of landing female crabs are the primary conservation measures. Additionally, escape ports in the crab traps reduce wastage. Season closures maintain product quality by reducing the harvest of recently molted crabs. Area closures reduce conflict between commercial and recreational fishermen.

Current management measures seem sufficient to prevent biological overexploitation but may not be optimal. Size limits reduce the necessity for a prohibition on harvest of females. Size limit levels may be too large when enforcement, optimum yield and genetic selection issues are considered. Consideration of the optimal level of effort in the crab fishery is complicated by the multispecies nature of the west coast's fishing fleet. High crab abundance during the late 1970s resulted in an increase in the size of the crab fleet and a large fraction of legal-sized male crabs are now harvested in the first few weeks of the season. Efforts to deal with this apparent overcapacity must consider the great mobility of vessels between the crab, salmon, albacore, shrimp, and groundfish fisheries.

En 1979, le Pacific Fishery Management Council a évalué la gestion de la pêche aux crabes dormeurs dans les États de la Californie, de l'Oregon et de Washington. Celle-ci peut être divisée en trois catégories, soit la conservation des ressources, le maintien de la qualité du produit et la limitation des conflits. Les principales mesures de conservation sont l'imposition de limites de taille et l'interdiction de débarquer des crabes femelles. De plus, des ouvertures spéciales pratiquées dans des casiers à crabes permettent de réduire les pertes. L'imposition de périodes saisonnières de fermeture permet de maintenir la qualité des produits en réduisant la récolte des crabes qui viennent de muer. L'interdiction de la pêche dans certaines zones aide à réduire les conflits entre pêcheurs commerciaux et sportifs.

Les mesures de gestion pratiquées à l'heure actuelle semblent suffisantes pour empêcher la surexploitation biologique mais ne sont pas nécessairement optimales. Les limites de taille réduisent la nécessité de l'interdiction de la récolte des femelles. Les limites de taille imposées pourraient toutefois être trop grandes en regard de la mise en application des règlements, du rendement optimal et de la sélection génétique. La question du niveau d'effort optimal pour la pêche des crabes est compliquée par le grand nombre d'espèces pêchées par les flottes de la côte Ouest. L'abondance de crabes durant la fin des années 1970 a entraîné un accroissement des flottes de caseyeurs et une grande partie des crabes mâles de taille réglementaire sont maintenant capturés durant les premières semaines de la saison de pêche. Afin de régler la question de cette surcapacité apparente, il faut se pencher sur la question de la grande mobilité des navires entre les lieux de pêche aux crabes, aux saumons, aux germons, aux crevettes et aux poissons de fonds.

Introduction

There are two striking characteristics of Dungeness crab fisheries on the United States' west coast: the fishery in central California (San Francisco area) collapsed in about 1960 to 10% of previous sustained landings and has not recovered, and the fishery in northern California (Eureka area) has oscillated with a period of about 10 yr and an amplitude of more than a factor of 10. Fisheries in Oregon and Washington also have oscillated but with lesser amplitude. Studies of stock dynamics in California (Peterson 1973; Botsford and Wickham 1974, 1978; McKelvey et al. 1980; Wild and Tasto 1983) have not conclusively demonstrated whether these fluctuations are environmentally driven or due to density-dependent mechanisms (Botsford 1986). Regulations intended to conserve the stock were first enacted by the State of California in 1897–1905 and have been modified little since then. These regulations have a biological basis (Miller 1976) but have not been quantitatively scrutinized for their effect on stock dynamics. The Pacific Fishery Management Council (1979), which manages fisheries in the U.S. Fishery Conservation Zone along the coasts of California, Oregon, and Washington, examined the status of crab fisheries and considered options for improved management, but no action was taken. This paper explores justification for current regulations and describes characteristics of the fishery with regard to current interest in control of the level of effort in this and other west coast fisheries.

Fishery History

A recent review of Dungeness crab fisheries in California (Dahlstrom and Wild 1983) identifies commercial landings at San Francisco in 1863 and a substantial fishery using hoop nets by the 1880s. Landings increased from 882 metric tons (t) in 1889 to 1662 t in 1899 then peaked at 2318 t in 1904. During this period there were indications of declining catch rates in the immediate vicinity of San Francisco and area of the fishery expanded. In response to concerns for conservation of the resource, possession and sale of female crabs was prohibited in 1897, a 2-mo closed season was enacted in 1903 and a minimum size limit became law in 1905. These regulations were insufficient to reverse the stock's decline. Landings from 1905 through 1913, although undocumented, apparently declined. When landing statistics became available again in 1915, landings had declined to about 100 t.

Dungeness crab catch at San Francisco remained low (200-900 t) through the 1923-24 season. In 1925-26 landings increased to the level observed in the 1890s but did not attain 2300 t again until 1948-49. Landings ranged from 1000 to 4000 t during 1949-60 (Fig. 1) then collapsed and have not recovered. Current landings, about 600 t, are similar to those of the early 1920s.

Much effort has been directed towards determining the cause of the collapse of central California's Dungeness crab stock in the early 1960s (Wickham 1979; Wild and Tasto 1983). However, the decline in landings during 1905-13 suggests that the 1960s' collapse was not an unique event. Wild et al. (1983) suggests that persistence of warm water and anomalous northward transport after the 1957-58 El Niño caused poor recruitment in central California. This correlation is logical because Dungeness crab in central California are near the southern limit of the species' range. It is possible that earlier changes in abundance of this stock also were due to climatic shifts. Unfortunately, consistent and continuous measurements of marine environmental conditions do not extend prior to the 1920s. Douglas (1980) used tree ring data to infer high air and sea temperatures in southern California during the mid-1800s and Hubbs (1948) noted extreme northward range extensions of many subtropical species during 1853-60. The Dungeness crab fishery which developed in central California during the late 1800s may have been possible because cooler environmental conditions (Douglas 1980) occurred then. Figure 10 in Douglas (1980) indicates warmer water occurred again during the early 1900s. These sparse and indirect data suggest that climatic conditions may play a role in determining abundance of Dungeness crab along the coast of central California.

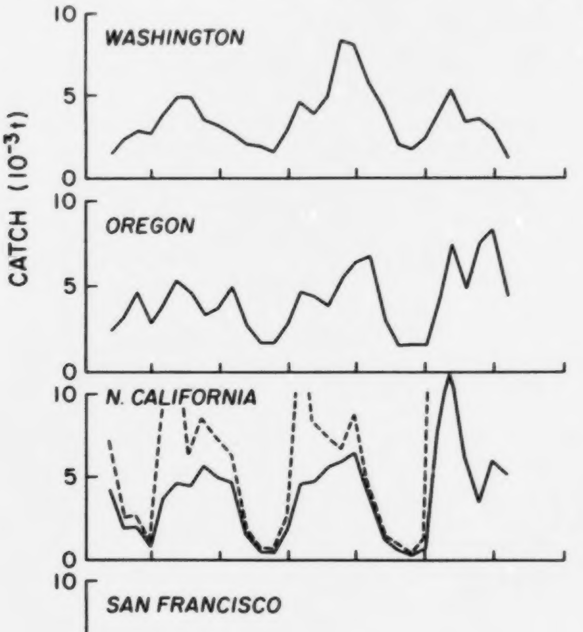

FIG. 1. Commercial landings of Dungeness crabs in California, Oregon, and Washington. Dashed line indicates pre-season abundance estimated form CPUE on cumulative catch (Methot and Botsford 1982). In northern California CPUE remained high throughout three seasons: 1956-57, 1965-66, and 1976-77, so pre-season abundance in these years must have been much greater than the catch.

A major Dungeness crab fishery did not start in northern California until the late 1930s. Expansion of this fishery began after 1941 when the canning prohibition and ban on export of Dungeness crab from several northern California counties were repealed. In the 1945-46 season the northern California catch first exceeded the central California catch. Since then northern California landings have oscillated between high catch periods of about 6 yr duration followed by low catch periods of about 4 yr (Fig. 1). Amplitude of the cycle has been increasing and the stock in 1984 seems near the end of the fourth high catch period which began in 1975-76. Landings off Oregon and Washington also exhibit a cyclic nature, but with lesser amplitude.

Development of Regulations

Management considerations in Dungeness crab fisheries include conservation of the resource, maintenance of product quality, and reduction in user conflicts. Regulations designed to achieve these goals now control size and sex of crab which can be landed, type of fishing gear, fishing areas and fishing seasons.

Concern over decline in stock abundance first became an issue in the San Francisco area during the 1890s. Possession and sale of female Dungeness crab by commercial fishermen was prohibited in 1897 to protect the resource from overfishing. This regulation remains in effect today in California, Oregon, and Washington. Only California's recreational fishermen may take female Dungeness crab.

Prohibition on female harvest preceded the size limit by 8 yr, but establishment of the size limit weakened the rationale for protecting females. Botsford (1984) concludes that the asymptotic mean size for females is 152 mm carapace width (excluding lateral spines) so few females are larger than the size limit. Females mature at about age 2 (90 mm) (Butler 1961) so they are mature for about 3 yr before approaching the legal size of 159 mm. Thus a size limit applied to males and females would have about the same effect as the current male size limit and female prohibition. Harvesting the few female crabs larger than 159 mm would increase yield little and may cause problems for industry because of claims (Pacific Fisheries Management Council 1979) that meat yields from female Dungeness crab are lower and that sexes would have to be separated before processing if females were landed.

The size limit for male crabs was established to protect crabs until they were mature, but there is no documented scientific analysis which determined the optimal size limit. In 1905 the limit was set at a carapace width of 152 mm (6 inches, including lateral spines). It is likely that processors' preference for large crabs was a factor in determining the level of this limit. The minimum was increased to 178 mm (7 in) in 1911 and the method of measurement was redefined slightly in 1915. In 1965 the measurement was redefined to 159 mm (6.25 in) excluding lateral spines without significantly changing the actual legal size of crab landed.

The size limit is an important constraint on the fishery. A large fraction of legal-sized male crabs are captured each year (Gotshall 1978a). Methot and Botsford (1982) examined decline in catch rate within each crab season and concluded that over 90% of legal-size male crabs were harvested in central California during each season from 1951 to 1955 and that exploitation rates greater than 80% were typical until 1964. In northern California, exploitation rate is commonly over 70%. Without the size limit a large number of smaller males also would be harvested and the possibility of overexploitation would be increased.

The appropriate size limit can be based on size at sexual maturity, yield per recruit, and enforcement problems if many crabs are near the size limit. Male crabs begin to mature at 108 mm and all males >122 mm sampled in California are sexually mature (Poole 1967) and are about 2 yr post-metamorphosis (Collier 1983). This size is 2 molts below the size limit of 159 mm (Table 1), so males have about 2 breeding seasons before entering the fishery. Size at maturity seems similar to that in the north (Collier 1983) but growth rate (molt frequency) is slower so northern males may have 3 breeding seasons before entering the fishery. Recruitment overfishing probably is not occurring and would not occur if the size limit was decreased.

The proximity of the male crab size limit to expected size at age 4 (Table 1) suggests that genetic selection for slow-growing individuals may occur. Larger age 4 males are available to the fishery and high exploitation rates (Methot and Botsford 1982) indicate that large, available males are unlikely to survive to the following mating season. Slow growing males will be below the size limit at age 4 so are likely to survive and mate for one more year. Genetic selection on male Dungeness crab could be reduced by lowering the size limit to about 150 mm so most age 4 male crabs would be available to the fishery.

Yield per recruit cannot be calculated for male Dungeness crab because growth and natural mortality data are not sufficiently precise. Growth of crabs older than about 4 yr is based primarily on molt growth increment data and does not take into account the fraction of older crabs that do not molt annually. The estimated size at age in Table 1 and size-weight relation in Botsford and Wickham (1978) indicate that weight at age of male crabs that molt annually increases by 71% from age 3 to 4 and by 57% from age 4 to 5. If natural mortality is about 0.50 (61% survival) then mortality would approximately balance growth for 3-5 yr-old male crabs, but natural mortality is not precisely known. An early estimate of 0.15 per year (Jow 1965) is remarkably low for an animal that seems to reach maximum size by age 6-7. Gotshall (1978) estimated natural mortality to be in the range 0.54 to 1.78, and the Pacific Fisheries Management Council (1979) considered values in the range 0.15-0.45. Given this imprecision, yield per recruit cannot guide establishment of the optimal size limit, but the data suggests that extreme growth overfishing is not occurring.

TABLE 1. Growth of male crabs at three locations along the west coast. Data are from Collier (1983) who included the earlier work of Butler (1961). Tabulated values are calculated carapace widths of males after the indicated molt (instar). Ages (yr) are from Botsford (1984). Age 1 occurs in November after hatching the previous winter.

Instar number	Age (yr)	Central California	Washington	Queen Charlotte Island
10		72.7 mm	68.0	72.7
11	2	90.0	84.6	90.2
108 mm — males begin to mature				
12		111.2	105.9	111.5
122 mm — all males are mature				
13	3	136.5	129.2	137.1
159 mm — males are available to the fishery				
14	4	163.0	154.9	164.5
15	5	190.9		193.7
16		220.3		224.9

Setting the size limit at a local minimum in the size distribution lessens enforcement problems by reducing incidence of crabs trapped near the size limit. Such an enforcement issue was considered in establishment of the size limit for Pacific bonito (Collins et al. 1980). On this basis the current size limit of 159 mm probably is too close to expected size at age 4 (Table 1). A limit of 150 mm is more nearly equidistant between expected size at ages 3 and 4 and could reduce enforcement problems associated with the size limit. Variation in growth (Botsford 1984) will make size modes less distinct and reduce the value of considering enforcement in setting the level of the size limit.

Other regulations assist in resource conservation. Some northern California bays and estuaries were closed to commercial crab fishing in 1933 and 1941. This regulation reduces conflict with recreational crab fishermen common in northern California bays and estuaries. In addition, prohibition of commercial crab fishing in northern California bays and estuaries, which have a high ratio of sublegal to legal size crabs, may reduce mortality of sublegal crabs associated with being captured and released. In central California, San Francisco and San Pablo bays are closed to commercial and recreational fishing to protect sublegal crabs.

Closed seasons conserve the resource by reducing harvest of soft-shelled (recently molted) crabs. If landed, these crabs would be a poor product and, if thrown overboard, they likely have higher mortality than hard crabs. The months of September and October were first closed in 1903. Currently season opening dates are: central California, second Tuesday in November; northern California, December 1; Oregon, December 1; and Washington, January 1 (but usually opens Dec. 1 by emergency regulation). Staggered opening dates are reasonable with regard to the north–south gradient in the date at which a high percentage of male crabs are hard (Pacific Fisheries Management Council 1979), but non-uniform opening dates cause enforcement problems. Closing dates now are in midsummer and vary somewhat among the states. Typically little fishing effort occurs during summer (Methot and Botsford 1982; Botsford et al. 1983) so the closing date has little effect on the fishery. Since 1981 California has experimented with season extensions through about August but little crab fishing effort occurred during the extensions.

Nearly the entire commercial crab harvest is taken in traps. In Washington and Oregon only traps and ring nets are legal gear. Gear restrictions are not specified in California but trawl vessels may have no more than 227 kg (500 lb) of Dungeness crab per landing. All three states require two escape ports in crab traps. These must be 108 mm (4.25 in) in diameter and be located in the upper half of the trap. Studies in Washington and Oregon (Pacific Fisheries Management Council 1979) indicate that this size retains nearly all legal-size crabs and releases many sublegals and females. Results of the Dungeness crab Research Program in California (Wild and Tasto 1983) indicate that an increase to 111 mm (4.375 in) would release about 50% more sublegal males and females with little increase in escapement of legal males. A change in the size limit to a local minimum in the size distribution should increase the effectiveness of escape ports.

About 10% of crab traps are lost each year. It is suspected that these traps continue to attract and capture Dungeness crab. California has a regulation requiring destruct devices on traps but implementation awaits development of a suitable device. The Dungeness crab Research Program (Wild and Tasto 1983) supported implementation of this regulation.

Commercial bottom trawling has been considered to be a source of mortality for Dungeness crab. Reilly (1983) monitored crab mortality aboard a commercial trawler in the San Francisco area. Overall mortality of crabs brought on deck was about 2% but soft-shelled male crabs had 20.2% mortality. The soft-shelled crabs often were crushed by the weight of the load of fish. Reilly (1983) lists several reasons why his observations probably underestimate crab mortality during normal fishing operations. Additionally, his study only addresses mortality of crabs retained by the net. Small crabs may be severely damaged as they pass through trawl mesh and recently molted crabs could be crushed by heavy trawl gear passing over them. California's Dungeness crab Research Program recommendation was to "Eliminate commercial trawl fishing in critical areas of the Gulf of Farallones during periods of peak molting (July–September) for male Dungeness crabs" (Wild and Tasto 1983). Fortunately, two factors reduce the likelihood of major crab mortality caused by bottom trawling. Trawlers cannot fish within 5.5 km (3 miles) of shore in California and they tend to fish in deeper water. Because Dungeness crab tend to occur in shallow water (Gotshall 1978b), much crab habitat is not vulnerable to bottom trawlers. Additionally, trawlers avoid crab areas because of the hazard presented to their nets by crab traps (Reilly 1983).

A second category of management measures concerns maintenance of product quality. Canning, pickling, or preserving crabs was illegal in the early years of the fishery and export of crabs from three northern California counties was prohibited (Dahlstrom and Wild 1983). The rationale for these regulations is uncertain but may be related to public health considerations because crab meat is highly perishable. Both of these regulations were repealed in 1941 and growth of the northern California Dungeness crab fishery began. The only current regulation affecting product quality is the closed season. Without this regulation a larger number of recently molted crabs, which have low meat yields, would be landed. Landing of softshelled crabs is prohibited in Washington.

The third category of management measures concerns reduction of conflict. Gear conflicts between crabbers and trawlers, salmon trollers and salmon gillnetters seems only a minor problem (Pacific Fisheries Management Council 1979). The crab fishery operates closer to shore than most trawl fisheries. In California trawling is prohibited nearshore in most areas and crab fishing extends into deep water only during the beginning of the season. The crab and salmon fisheries are separated in time. Little crab fishing occurs after opening of the salmon season in April or May.

Conflict, or at least competition, may occur between commercial and recreational crab fishermen. Regulations to reduce conflict between users include area closures and gear limitations. In Washington some areas of Puget Sound are closed to commercial crab fishing and the entire sound has a limit of 100 traps or ring nets per boat. In Oregon use of traps is prohibited in five major bays. In California major bays and estuaries are closed to commercial Dungeness crab fishing and this area closure extends 1.85 km (1 mile) into the open ocean at two northern California locations. These regulations tend to separate commercial and recreational fishing areas and greatly reduce the commercial fishing activity in juvenile crab nursery areas.

Current Fishery

Dungeness crab is one of the most valuable fisheries on the U.S. west coast. During 1980–83 the value of crab landings in northern California (Table 2) was exceeded only by the groundfish complex (flatfish, rockfish, cod, sablefish). Landings of shrimp during 1980–83 are down from their historical high during the late 1970s and salmon and albacore landings fluctuated by

TABLE 2. Value of landings ($US 10^{-3}) in central (San Francisco area) and northern (Eureka area) California in recent years. Data are preliminary and are subject to modification (California Dep. of Fish and Game).

	1980		1981		1982		1983		Mean	
	N.CA	C.CA	N.CA	C.CA	N.CA	C.CA	N.CA	C.CA	N.CA	C.CA
Crab	9127	590	6902	475	6606	638	6926	994	7390	674
Salmon	6861	4632	7590	5549	9150	7247	1966	1115	6392	4636
Albacore	1212	1107	4189	4212	625	358	731	1732	1689	1852
Groundfish	9342	3367	9873	4393	11742	6186	9216	4900	10044	4707
Shrimp	1318	1	1512	8	2058	3	147	0	1259	3
Herring	156	16416	56	4570	61	9647	45	12437	80	10768
Other	952	863	567	395	1018	1483	335	1028	718	942
Total	28968	26976	30689	19602	31260	25562	19366	22206	27571	23587

about a factor of 5 (Table 2). On a 10-yr time scale the value of Dungeness crab landings also has oscillated about 5-fold, even though changes in price tend to buffer the value of landings from fluctuations in catch (Botsford et al. 1983). During the 1968–69 and 1969–70 seasons the average value in California was $3,940,000 ($3.94 M), during the 1971–72 and 1972–73 seasons the average value was $1.17 M and during the 1979–80 through 1982–83 seasons the average value was $8.06 M (Table 2). The Dungeness crab fishery appears sufficiently valuable to warrant attention of fishery managers.

Evidence presented earlier suggests that current regulations are sufficient to prevent overexploitation of the stock. Recruitment overfishing seems unlikely with the prohibition on female landings and the size limit on males; growth overfishing probably is not occurring but yield per recruit cannot be estimated with available data. Changes in management should not be expected to improve the magnitude of the harvest. The low level of the central California stock and the large amplitude oscillations of the northern stocks currently must be treated as conditions which fishermen and managers react to, but do not control.

A major problem in the west coast's Dungeness crab fisheries is the large capacity of the fleet. West coast fishermen tend not to specialize so any attempt to redistribute excess crab fishing effort requires knowledge of the Dungeness crab fishing fleet in relation to other west coast fisheries. The following section will describe the characteristics and mobility of the crab fishing fleet, then the problem of excess fishing effort will be reexamined.

Dungeness crab tends to be fished by small, multipurpose vessels. Crab vessels usually are converted salmon trollers or bottom trawlers (Frey 1971) and may shift to other fisheries during the off-season for crab and during poor crab fishing years. In a 1968 survey, the mean lengths of crab vessels were 11 m in central California and 12 m in northern California (Dahlstrom and Wild 1983). The Pacific Fishery Information Network, PACFIN, database (Huppert et al. 1984) provides an opportunity for examination of the crab fleet composition during 1981.

In 1981, 1439 vessels landed Dungeness crab. Vessels were categorized into high and low income groups based on total exvessel value of all species, into principal species groups based on the species which contributed the greatest fraction of the vessel's total value and into regions based on the port at which the vessel landed the greatest value. Low income vessels (< $10,000 exvessel value) were small, about 9 m, and landed only 6.3% of the Dungeness crab in 1981. High income vessels with Dungeness crab as their principal species composed 31% of the crab fleet (Table 3) and landed 66% of the crab (Table 4). These vessels averaged 11.7 m in length. High income vessels with a species other than crab as their principal species landed the second highest fraction of crab, 28%, and composed 33% of the crab fleet. These vessels were slightly larger, 12.8 m, than the principal crab vessels. Much of the crab catch by high income, principally non-crab vessels was by 15–30 m vessels fishing in Oregon and northern California (Table 4). These larger multispecies vessels seem to be the major change in composition of the crab fleet between 1968 and 1981.

In 1981, 51% of high income vessels which landed crab obtained more income from another species. Fishermen may shift to different fisheries within and between years. Within year shifting is facilitated by the limited duration of several fisheries. Crab, salmon, shrimp, and herring fishing are limited by seasonal closures and albacore fishing is limited by seasonal migration pattern (Table 5). The timing of these seasons is sufficiently staggered so that a fisherman can fish during the peak of the crab, salmon and albacore seasons or the crab and shrimp seasons. The importance of within season switching in 1981 can be considered with the PACFIN database (Huppert et al 1984). The high income vessels which landed crab comprised only 6% of the fleet but landed substantial fractions of other species groups (Table 6): herring, 8%; groundfish, 12%; salmon, 13%; albacore, 19%; and shrimp, 37%. The high value for shrimp may be due to depressed shrimp landings since the late 1970s. This latter factor may have reduced the number of vessels which target on shrimp so those vessels which fish crab and shrimp land a large fraction of the total shrimp. This argument suggests that between year shifting out of the shrimp fishery has influenced the analysis within 1981. In years with poor salmon or albacore catch (i.e. 1983, Table 2), it is likely that a higher fraction of the catch of these species is

TABLE 3. Sizes of fishing vessels in 1981. Vessels are categorized according to total exvessel value of their landings (< or > $10,000), to the state of their principal port and their principal species. Principal port is defined by the total exvessel value of landings. Principal ports in California are divided at Monterey into a south region and a north region which contains the San Francisco and Eureka areas. Principal species is determined by the exvessel value of each species landed: CRAB+ indicates that a vessel's principal species was crab, CRAB− indicates that the principal species was not crab but some crab were landed, CRAB0 indicates that no crab were landed by that vessel in 1981. Weighted mean vessel length uses the vessel's crab catch as the weighting factor. Data are from the annual vessel summary file of the 1981 PACFIN database (Huppert et al. 1984).

	Vessel length class (m)					Length (m)	
	0-9	10-15	16-21	>21	Total Number	Mean	Wt. mean
		Exvessel value < $10,000					
CRAB+							
WA	141	41	3	0	185	8.1	8.4
OR	21	40	2	4	67	11.5	11.9
N.CA	62	42	3	1	108	9.4	10.2
TOTAL	224	123	8	5	360	9.1	9.6
CRAB−							
WA	25	10	0	0	35	9.0	8.9
OR	27	19	1	0	47	9.2	9.1
N.CA	46	20	1	0	67	8.9	8.8
S.CA	1	1	0	0	2	9.8	9.8
TOTAL	99	50	2	0	151	9.0	8.9
CRAB0							
TOTAL	8494	2463	140	39	11136	8.3	—
		Exvessel value > $10,000					
CRAB+							
WA	32	63	3	0	98	10.7	12.0
OR	22	145	8	1	176	11.7	12.0
N.CA	30	129	17	1	177	12.2	13.2
TOTAL	84	337	28	2	451	11.7	12.5
CRAB−							
WA	21	45	5	0	71	11.4	12.1
OR	21	93	43	7	164	13.8	15.9
N.CA	30	168	26	6	230	12.5	15.4
S.CA	3	6	2	0	11	11.7	15.9
TOTAL	75	312	76	13	476	12.8	15.4
CRAB0							
TOTAL	669	1480	458	216	2823	14.1	—

by vessels that also fish crab. Conversely, in years with low crab abundance a large amount of effort must shift to other fisheries. Continuation of the PACFIN database for several years should provide the information necessary for separation of between and within year shifts in effort. Better definition of between and within year effort shifting is critical as schemes to control effort in these fisheries are evaluated.

The number of vessels landing Dungeness crab in northern California has fluctuated similarly to the 10-yr cycle of catch (Botsford et al. 1983). At low points in the catch cycle (1954–55, 1963–64, and 1973–74) only 95, 117, and 93 vessels respectively have fished Dungeness crab. By the end of each high catch period the number of vessels had doubled: 196 vessels in 1951–52, 213 vessels in 1960–61, and 250 vessels in 1970–71. At the onset of the current high catch period in the 1975–76 season, the number of vessels increased at an unprecedented rate (299 vessels in 1975–76) and during the calendar year 1981, 418 high income vessels and 177 low income vessels fished crab in California (Table 3).

The number of vessels in the fishery influences seasonal distribution of catch (Table 7). The fraction of the season's catch landed in December through February has fluctuated between 50% and 90% during the 1960s–early 1970s (Methot and Botsford 1982). Higher values tend to occur at the end of the high catch periods as the number of vessels increases and at the beginning of the low catch periods as the vessels' exit from the fishery lags behind the decline in abundance (Botsford et al. 1983). Catch during the final months of the season tended to parallel the total season catch. This indi-

TABLE 4. Total crab landings (t) by vessels in 4 length categories. The vessels also are categorized according to total value of landings, the state of their principal port and whether their principal species was crab. See Table 3 for definition of categories. Data are from the annual summary file of the PACFIN database (Huppert et al. 1984).

	Landings (t)				
	Vessel length class (m)				
	0–9	10–15	16–21	> 21	Total
	Exvessel value < $10,000				
CRAB+					
WA	204.7	76.1	4.1	—	284.9
OR	28.8	71.0	4.7	7.1	111.7
N.CA	65.4	59.9	9.7	1.0	136.0
TOTAL					532.5
CRAB−					
WA	14.5	4.6	—	—	19.1
OR	11.2	8.4	0.1	—	19.8
N.CA	21.6	7.9	0.3	—	29.8
S.CA	0.1	0.1	—	—	0.2
TOTAL					68.9
	Exvessel value > $10,000				
CRAB+					
WA	209.1	955.7	57.3	—	1222.2
OR	169.4	1883.2	128.9	5.9	2187.3
N.CA	284.1	2085.9	454.4	32.6	2857.0
TOTAL					6266.6
CRAB−					
CA	43.5	157.3	9.4	—	210.3
OR	34.7	626.1	525.3	76.0	1262.2
N.CA	51.4	663.3	274.8	194.3	1183.8
S.CA	1.1	1.0	43.2	—	45.2
TOTAL					2701.5

TABLE 5. Seasonal distribution of landings (t) of major species groups which have strong seasonal patterns. The seasonal patterns for these species, except albacore, are dictated by closed fishing seasons. The tabulated values are for all of California in 1981 (preliminary data obtained from California Dep. of Fish and Game).

	Landings (t)				
	Crab	Salmon	Albacore	Herring	Shrimp
JAN.	657	0	0	2962	0
FEB.	244	0	9	1216	1
MAR.	79	0	<1	83	0
APR.	109	0	3	0	<1	375
MAY	64	767	0	<1	450
JUNE	20	287	5	<1	230
JULY	6	893	532	6	209
AUG.	7	602	3210	84	199
SEPT.	<1	179	3157	0	289
OCT.	<1	<1	1648	<1	97
NOV.	54	0	259	0	1
DEC.	2477	0	7	1492	1

cates that large early season harvests, which occurred in some high catch years, were not large enough to depress the late season harvests.

During the 1980s the late season catch was low despite high total season catches (Table 7). The number of vessels in the crab fishery is at a record high and the fraction of the total season catch landed during December through February also is at record levels. The fraction landed during December alone is at a very high level: 1980–81, 86%; 1981–82, 66%; and 1982–83; 77%.

The probable cause of the low late season harvests is reduction in abundance of legal-sized males caused by the large early season harvest. Historically the fishery has been able to land up to about 90% of legal males in a season (Methot and Botsford 1982). Currently they seem able to achieve this exploitation rate in the first few months of the season. Another possible cause for low late season catches is increased within year shifting of effort. As the catch rate of crab declines within the season the multi-purpose fishing vessels may be capable of making more money by shifting effort to salmon, shrimp or groundfish. Thus increased participation by multi-purpose fishing vessels may have exaggerated the within season fishery dynamics.

Packing the catch into the first few weeks of the season has several adverse consequences: competition between fishermen increases as each deploys more gear to get a share of the harvest, processors must freeze

TABLE 6. 1981 landings in California, Oregon and Washington of 6 important species groups by 6 categories of fishing vessels. CRAB+ vessels obtained most of their income in 1981 from Dungeness crab. CRAB− vessels landed some Dungeness crab but obtained most of their income in 1981 from a different species group. CRAB0 vessels did not land Dungeness crab in 1981. These data are from the annual summary file of the 1981 PACFIN database (Huppert et al. 1984)

Species group	Vessels with < \$10,000			Vessels with > \$10,000			TOTAL (t)
	CRAB+	CRAB−	CRAB0	CRAB+	CRAB−	CRAB0	
	Percent of landings						
Crab	5.6	0.7	0	65.5	28.2	0	9569
Salmon	0.3	0.8	25.9	4.2	8.8	60.0	17817
Albacore	<0.1	0.1	3.3	5.0	13.7	77.9	12973
Groundfish	<0.1	<0.1	1.1	1.0	11.1	86.7	113691
Shrimp	<0.1	<0.1	0.2	4.2	32.4	63.2	18139
Herring	<0.1	0.3	6.2	0.9	7.1	85.5	7013
	Percent of vessels						*N* vessels
	2.3	1.0	72.3	2.9	3.1	18.3	15405

TABLE 7. Trends in catch and effort in the northern California (Eureka area) Dungeness crab fishery (Methot and Botsford 1982; Botsford et al. 1983). Data for the seasons 1980–81 through 1982–83 are preliminary figures from the California Dep. of Fish and Game.

Season	Total catch (t)	Percent in Dec.–Feb.	Catch in May–Aug. (t)	*N* Vessels
1960–61	4555	75	382	213
1961–62	1475	90	70	190
1962–63	409	82	29	124
1963–64	370	66	39	117
1964–65	1805	72	89	164
1965–66	4528	53	332	169
1966–67	4672	73	271	168
1967–68	5508	86	186	173
1968–69	5828	85	337	194
1969–70	6397	81	318	237
1970–71	3555	42[a]	476	250
1971–72	1153	88	87	190
1972–73	523	80	59	153
1973–74	160	46	26	93
⋮				
⋮				
1980–81	4691	99	31	—
1981–82	3672	94	50	595[b]
1982–83	1915	90	22	—

[a] Low harvest in January, probably price dispute between fishermen and processors.

[b] Number of crab vessels in calendar year 1981 from PACFIN database (Huppert et al. 1984).

more crab for longer periods, and distributors have only a brief supply of fresh crab. The foreshortened season may be the major problem with the Dungeness crab fishery (Meyer Resources Inc. 1983), but effort management schemes which would distribute the catch more evenly over the season will be difficult to evaluate and implement. The great decline in crab catch per effort within in each season (Methot and Botsford 1982) and the seasonal availability of opportunities to shift into other fisheries are two obvious complicating factors.

Excess capacity in the Dungeness crab fleet also may indicate a situation of economic overfishing. Total harvest seems to be divided among too many fishermen so the average profit per fisherman is less than it could be. Schemes for reducing effort in the crab fishery were considered by the Dungeness Crab Project of the State/Federal Fisheries Management Program (Collinsworth and Silverthorne 1976). The Project attempted to determine optimum level of effort (number of traps) for the coastwide fishery and considered three means of regulating effort at an appropriate level: licensing vessels and/or traps, taxes on landings, and quotas for individual fishermen. The Project did not explicitly consider the multispecies aspect of this fishery. The propensity of fishermen to shift effort between fisheries confounds economic analysis of effort limitation in any one of the fisheries. The concentration of crab fishing effort into the early part of the season may not be the optimal scheme for harvesting the crab resource, but fishing heavily on crab then shifting to other species may be the optimal multispecies fishery. An additional complication, if a license or individual quota scheme is to be implemented, is determining current fishery participants. This determination is hindered by the between and within year shifting of effort between fisheries. Not all potential crab fishermen will fish crab every year.

Interviews with fishermen indicate that crab fishermen do not feel that a major problem exists in the crab fishery (Meyer Resources Inc. 1983). The overcapacity problem is greater in the salmon fishery and recent poor shrimp abundance has created overcapacity in that fishery. The problem in the crab fishery is the shift of vessels from these other fisheries into the crab fleet.

The anticipated decline in crab landings over the next few years will have repercussions outside of the crab fishery. The great capacity of the current crab fleet probably will not hinder a recovery of the stock; the female prohibition and male size limit seem more than adequate to protect the reproductive potential of the stock. However, while the stock is at the low level, fewer vessels will be able to fish crab profitably. Vessels which currently are not able to operate profitably in the salmon or shrimp fisheries will not have the option of supplementing their income by fishing crab during the winter. As vessels leave the crab fleet during the mid 1980s, there seem few opportunities for them in other species. If the Pacific Fisheries Management Council is to consider management of the effort in the salmon and groundfish fleets, they must simultaneously consider the Dungeness crab fishery.

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Differential Susceptibility of Atlantic Snow Crab, *Chionoecetes opilio*, Stocks to Management

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A review of the snow crab, (*Chionoecetes opilio*), fisheries in the Gulf of St. Lawrence and around Cape Breton Island reveals a paradoxical array of responses to the same management regime; production and abundance appear to have increased under heavy fishing pressure in one stock, remained stable in another, while a third collapsed. Although exploitation is focused exclusively on mature males and high fecundity levels appear to have been maintained, recruitment has been unpredictable. We discuss the possible roles of various abiotic and biotic factors as phenomena responsible for the recruitment trends. Presently, the incongruous nature of snow crab population dynamics, as manifested under exploitation, has preempted recruitment forecasting and confounded effective management.

Un examen de la pêche du crabe des neiges (*Chinoecetes opilio*) dans le golfe Saint-Laurent et autour de l'Île du Cap-Breton révèle un paradoxe dans les réactions au même système de gestion; la production et l'abondance semblent avoir augmenté dans un stock soumis à une forte pression de pêche et sont demeurées stables dans un autre, tandis qu'un troisième stock a connu une forte baisse. Bien que l'exploitation vise exclusivement les mâles adultes et qu'il semble que les niveaux élevés de fécondité aient été maintenus, le recrutement a été imprévisible. Nous discutons du rôle que peuvent jouer divers facteurs biotiques et abiotiques en ce qui concerne les tendances observées dans le recrutement. Pour le moment, l'incohérence de la dynamique des populations de crabe des neiges, telle que démontrée dans des conditions d'exploitation, ne permet pas de prévoir le recrutement et empêche une gestion efficace.

Introduction

Exploitation of snow crab, *Chionoecetes opilio*, in Atlantic Canada started in 1960 with incidental bycatches by groundfish draggers off Gaspé, Quebec (Brunel 1961; Watson 1970a). Annual landings have increased rapidly since the inception of a directed trap fishery in 1966 after exploratory vessels located extensive new grounds in the Gulf of St. Lawrence (Table 1). The peak landings of 47 004 t in 1982 were worth over $43 million to the fishermen, and placed snow crab fourth in landed value in the Canadian Atlantic fishery behind cod, lobsters and scallops. The 37 255 t of snow crab landed in 1983 had a record landed value of over $53 million.

Harvesting of snow crab in Atlantic Canada is through a directed single-species fishery by approximately 390 licensed vessels with baited traps as their sole gear type (Elner 1982a). The principal fishing grounds are on mud or sand-mud bottoms between 60–380 m and are located in the St. Lawrence estuary and Gulf, around Cape Breton Island and off the east coast of Newfoundland (Fig. 1). Vessels under 13.7 m length fish the inshore grounds in the Gulf of St. Lawrence and around Cape Breton Island where 1-d trips are feasible. These vessels engage in other fisheries, particularly the American lobster (*Homarus americanus*) fishery, depending on season and earnings. Vessels ranging from 13.7 to 21.3 m length with the capability of making up to 3-d trips to offshore grounds and devoted to exclusively fishing snow crab account for the majority of landings.

Mark–recapture studies off Newfoundland and Cape Breton Island have not revealed either extensive or clear patterns of movement by mature male snow crabs (Elner 1982a; D. M. Taylor, unpublished data). In the Gulf of St. Lawrence, the majority of marked snow crabs have been recaptured within 15 km of the release point (Watson 1970b; Watson and Wells 1972). Although exchanges of mature snow crabs between the principal fishing grounds are unlikely, the fact that larvae are planktonic for 3–4 mo and probably subject to dispersion by ocean currents, makes recruitment relationships between the grounds a possibility (Davidson et al. 1982; Davidson 1983).

An important feature of the Atlantic snow crab fishery is that the legal minimum size of 95 mm carapace width (CW) focuses exploitation onto mature male crabs (Elner and Robichaud 1983a). Female snow crabs attain a maximum size of between 47–95 mm CW (Watson

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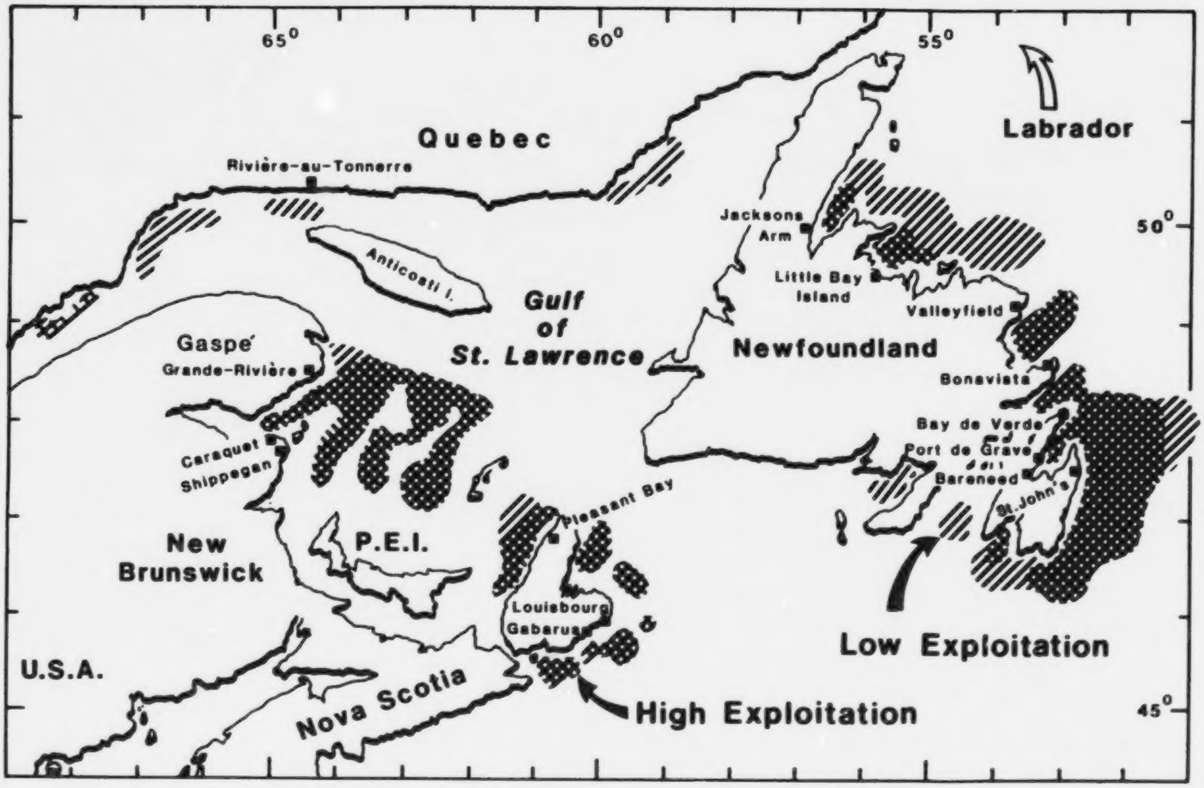
65°
60°
55°
Quebec
Labrador
Rivière-au-Tonnerre
50°
Jacksons Arm
Anticosti I.
Little Bay Island
Gulf of St. Lawrence
Valleyfield
Gaspé
Grande-Rivière
Newfoundland
Bonavista
Bay de Verde
Port de Grave
Bareneed
St. John's
Caraquet
Shippegan
Pleasant Bay
New Brunswick
P.E.I.
Louisbourg
Gabarus
Low Exploitation
U.S.A.
Nova Scotia
High Exploitation
45°

FIG. 1. Distribution of snow crab fishing grounds in Atlantic Canada, 1983.

1970a). Mating generally occurs between a hard-shelled male snow crab and a soft-shelled female soon after the female's molt to puberty; at least two successive egg clutches may be extruded from the sperm received (Watson 1970a, 1972). Male snow crabs reach maturity at 51–80 mm CW and are able to mate in the intervening 1–4 yr before attaining the legal minimum size for entry into the fishery. The fact that >90% of mature females caught are ovigerous indicates that egg production is being maintained at a high, pre-fishery level despite heavy exploitation of large males (Elner and Robichaud 1983a; Elner and Gass 1984).

Although the whole Atlantic snow crab fishery is under the same basic management regime, a review of the various stocks reveals a paradoxical array of responses to exploitation: ranging from increase in stock size to stock collapse. The present paper examines the management regime for Atlantic snow crab, explores the differing dynamic responses of three snow crab stocks to exploitation and reflects on the management implications of such a seemingly paradoxical scenario.

MANAGEMENT: RATIONALE AND REGULATION

The Atlantic snow crab resource is under the jurisdiction of the Federal Government of Canada and is managed through the Department of Fisheries and Oceans. Although the snow crab fishery started in the 1960's, there were few restrictions on effort or gear until regulations were enacted in 1976. The regulations and their rationales are discussed in-depth by Miller (1976, 1977). The actual resource management strategies in effect to optimize yield can be arbitrarily categorized into "resource conservation" and "resource allocation" initiatives.

The rationale for the resource conservation measures is to ensure the renewal of the resource by protecting female and sublegal-sized male snow crabs. This is attempted by:

1) Regulations that state all females caught in traps must be returned to the sea.
2) Regulations that prohibit possession of any snow crab of less than 95 mm CW.
3) Regulations, enforced in the Gulf of St. Lawrence and Cape Breton Island fisheries, that state two side panels of each rectangular trap must be covered with netting of at least 131 mm mesh size to facilitate escapement of females and sublegal-sized male snow crabs. In Newfoundland, mesh size must be at least 114 mm.

The rationale for the resource allocation measures is to promote biological and economic stability thus ensuring all participants a sustained, reasonable income from the fishery. Stability has been pursued by enacting various effort controls to contain the exploitation rate on the exploitable portion of the resource at moderate levels (50–60%). Higher exploitation rates would result in increased dependence on newly recruited crabs, most of which would be caught as recently molted, soft-shelled crabs unacceptable to processors. The moderate exploitation rate strategy is designed to approximately achieve maximum yield-per-recruit while promoting stability in annual landings by reducing dependence on the vagaries of recruitment. Concommitantly, catch rates should be expected to remain higher and more stable under moderate rates of exploitation than under high exploitation rates. Resource allocation controls are summarized as follows:

1) Control of the size and number of participating vessels by strictly limiting the number and type of snow crab licenses issued.
2) Control of the number of traps fished by each vessel. The maximum rectangular trap limit is 150 in the southwestern Gulf, 50 in the northern Gulf and 30 around Cape Breton Island. Vessels in Newfoundland may use up to 800 conical traps.
3) Control of the number of vessels in a given area by establishing fishing zones. Such zones are enforced around Cape Breton Island, along the north shore of the Gulf and off Newfoundland to help better distribute the resource amongst local fishermen.
4) Control of the period in which fishing takes place by imposition of seasons. Off Cape Breton Island, regulations limit the season to 8-wk, mid-July to early September; the relatively short season is in accord with developing this particular fishery as a supplementary fishery with a large number of participants. Given favourable ice conditions, crab fishing may continue almost year-round off Newfoundland, except for a legal closure in January. The snow crab season in the Gulf of St. Lawrence is not defined by regulations and lasts approximately 6 mo, extending from ice breakup in April to the onset of adverse weather in November. Closure and manipulation of fishing seasons has been used to circumvent soft-shelled crab quality problems.
5) Control of the amount of crab landed by imposition of a total allowable catch (TAC) partitioned into individual vessel quotas. Management has contained exploitation to moderate levels off the NW coast of Cape Breton Island by permitting harvest of TAC's equivalent to the estimated average annual biomass increases resulting from growth and recruitment. Preemptive action to stabilize stocks has been taken occasionally in other areas by enforcing TAC's that are designed to restrict landings to moderate levels until the stock's dynamics can be modelled to permit more optimal exploitation.

Annual assessments are carried out on the basis of logbook, mark–recapture, research cruise and commercial sampling data. Assessments are subject to peer review through two levels of the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC). Management considers CAFSAC-generated advice in context with socioeconomic factors before making recommendations for enactment. Regional snow crab advisory committees, made up of representatives from fishermen, processors, and the provincial and federal governments serve as a link between industry and government and may debate or propose management regulations.

ASSESSMENT METHODOLOGY

Commercial snow crab catches are sampled regularly at landing points throughout Atlantic Canada and sales slips are analysed to provide total landings (Bailey 1983a; Parsons et al. 1983; Rowell 1983). Sampling is also carried out at-sea onboard licensed crab vessels and commercial vessels, such as danish seiners, that have a crab by-catch. Most importantly, data are analysed from fishermen's logbooks. The mandatory logbooks provide crucial details such as daily catch weight, number and type of traps hauled and trap location. Tagging programs are used to elucidate commercial stock sizes, exploitation rates, movements and growth.

Snow crab stock assessments are routinely made with the Leslie method (Leslie and Davis 1939; Braaten 1969). The Leslie methodology involves extracting logbook data and regressing mean CPUE ($\mathrm{kg \cdot trap\ haul^{-1}}$) against cumulative captures through a fishing season. The intercept of the regression line on the cumulative catch axis is an estimate of the initial stock size and the slope is an estimate of the catchability (q) of the gear. The exploitation ratio is estimated by dividing the total captures by the initial stock size.

If q is assumed to be constant throughout the fishing season, then the biomass (B_t) present at any given time is found from:

$$(1) \quad B_t = \frac{\mathrm{CPUE}_t}{q}$$

where CPUE_t is the mean CPUE at that time.

Equation (1) makes it possible to estimate biomass increases from growth and recruitment, through molting, during the fishing season. Significant molting periods are detectable by rises in mean CPUE and simultaneous increases in the frequency of soft-shelled crabs in commercial catch samples and are excluded from the Leslie regression per se. Generally, effort is not standardized for soak time in the assessments as logbook data is usually not amenable to such resolution. Nevertheless, the effects of soak time on Leslie estimates were investigated by Bailey and Cormier (1983a, 1983b); their estimates for known soak times were close to the estimates generated with non-standardized soak time data.

Ricker (1975) and Bailey (1983b) give detailed accounts of the inherent assumptions and possible sources of discrepancy implicit in the Leslie method. However, Petersen estimates of snow crab stock size from mark–recapture studies have provided independent corroboration of Leslie estimates (Bailey 1978a) and support the contention that the methodology is a robust and practical tool.

The Cape Breton Island Experience

Exploitation of the snow crab resource around Cape Breton Island, Nova Scotia, was started in 1966 by inshore vessels trapping off the NW coast (Fig. 2). Between 1977 and 1979, landings rose markedly in phase with effort and the expansion of the fishery around most of the Island's coast. Six inshore areas have been defined around Cape Breton Island (Fig. 2) for exclusive exploitation by inshore vessels less than 13.7 m, length. One hundred and forty-nine inshore vessels were partitioned between these areas in 1983.

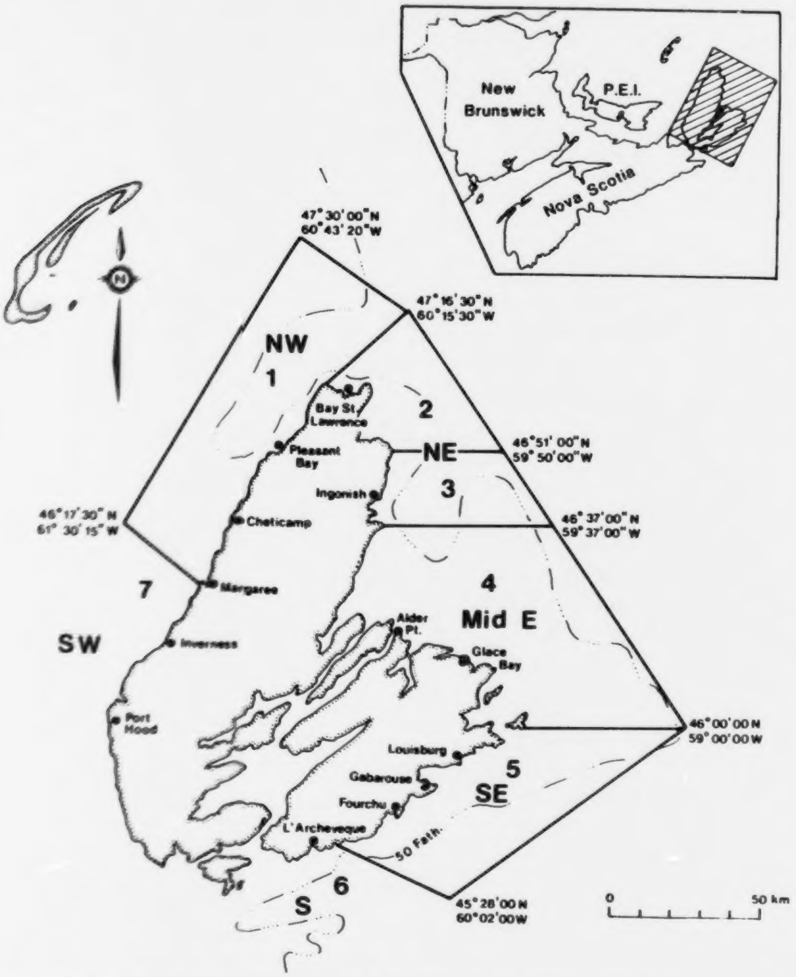
New Brunswick
P.E.I.
Nova Scotia
47°30'00"N
60°43'20"W
47°16'30"N
60°15'30"W
NW
1
Bay St. Lawrence
2
Pleasant Bay
NE
46°51'00"N
59°50'00"W
Ingonish
3
46°17'30"N
61°30'15"W
Cheticamp
46°37'00"N
59°37'00"W
7
Margaree
4
Mid E
Alder Pt.
SW
Inverness
Glace Bay
Port Hood
46°00'00N
59°00'00W
Louisburg
5
Gabarouse
SE
Fourchu
L'Archeveque
50 Fath.
6
S
45°28'00N
60°02'00W
0
50 km

FIG. 2. Snow crab management areas around Cape Breton Island.

Additionally, 25 inshore vessels were licensed to fish area 7 off the SW coast; area 7 is also open to the New Brunswick and Quebec offshore crab fleets. The major commercial concentrations of snow crab around Cape Breton Island are on the Gulf of St. Lawrence-coast grounds (area 1 and 7); the 52 inshore fishermen in these areas accounted for 78% (1728 t) of the total snow crab landings (2209 t) recorded for Cape Breton Island (areas 1–7) in 1983. In comparison, since 1980, the 122 licensed fishermen on the Atlantic coast of the Island (areas 2–6) have been largely confined to exploiting scattered, low-density pockets of snow crab.

Utilizing the various monitoring data, annual stock assessments have been produced by Bailey (1978a), Elner (1982b), Elner and Robichaud (1980, 1981, 1983b, 1984), Bailey and Cormier (1983a). Based on the annual stock assessments, we appraise the snow crab fishery and stock dynamics in area 1, representative of the Gulf of St. Lawrence-coast grounds, and area 5, representative of the Atlantic-coast grounds.

NW Cape Breton Island (area 1)

A TAC of 1406 MT was set for area 1 in 1979, based on an assessment of commercial biomass additions during the previous season. Similarly, based on the assessment for 1979, a TAC of 980 t was set for the 1980 season. The 1980 TAC was subsequently raised to 1224 t following high catch rates during the initial weeks of the season. Since 1980 the TAC has been maintained at 1000 t. Seasonal landing patterns since 1978 reflect a stable landing trend with the bulk of the catch being achieved during the initial 4 wk of the fishing season (Fig. 3).

Patterns in mean CPUE through the fishing season have been similar in shape and range over the past 6 yr and reflect the general stability of the area 1 snow crab resource (Figs. 4,5). Overall, stability appears to have been achieved as a result of annual growth and recruitment levels having been approximately balanced by annual removals by the fishery (Table 2).

SE Cape Breton Island (area 5)

A preemptive TAC of 943 t was set for area 5 in 1980. In 1981, a TAC of 41 t, equal to the estimated between season growth and recruitment in 1979–80, was advised in an effort to stabilize the diminishing stock. However,

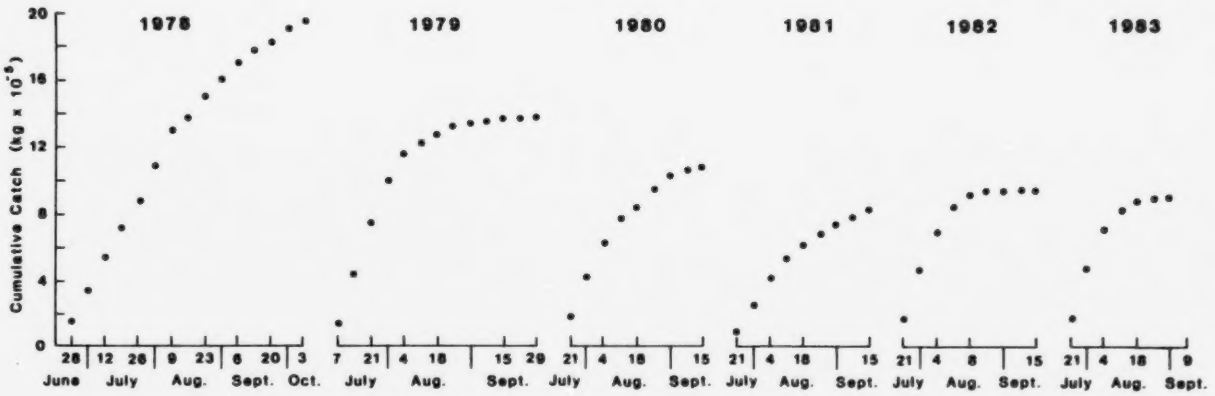

FIG. 3. Historical trends in cumulative snow crab landings, from logbook data, over time, for area 1, NW Cape Breton Island, 1978–83.

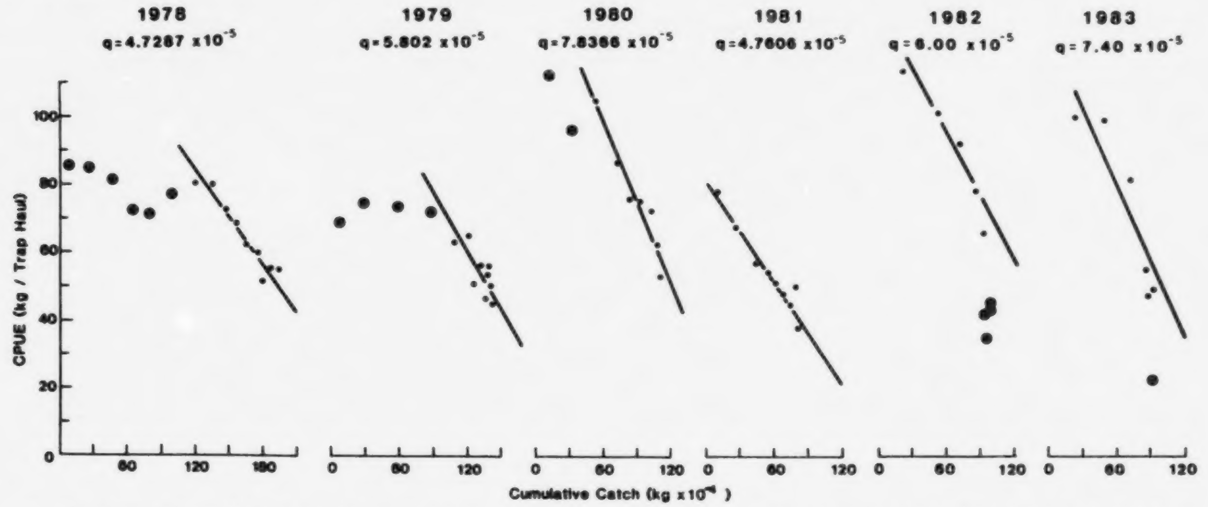

FIG. 4. Historical trends in mean weekly CPUE over cumulative snow crab landings, from logbook data, for area 1, NW Cape Breton Island, 1978–83. Note data points and regression lines used in Leslie analyses.

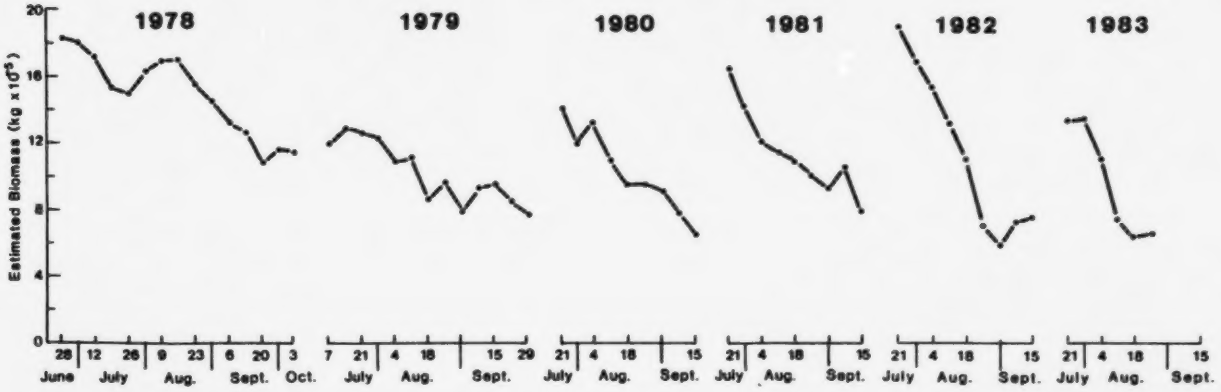

FIG. 5. Historical trends in estimated commercial biomass of snow crabs, derived from Leslie analyses of logbook data, over time, in area 1, NW Cape Breton Island, 1978–83.

a review of assessment data suggested that the area 5 snow crab resource represents a marginal, low-productivity system from which most of the accumulated virgin biomass had been removed by the fishery. Consequently, and on the assumption that the reproductive potential of the stock would be protected by the minimum legal size regulation, the stock stabilization strategy was abandoned and the fishery has been conducted on an opportunistic basis since 1982. TAC controls have been dropped and the existing fishermen have

TABLE 1. Estimated snow crab landings and landed values for Atlantic Canada, 1966–83.

Year	SW Gulf of St. Lawrence (New Brunswick, Quebec) (t)	Cape Breton Island (Nova Scotia) (t)	Atlantic Canada total[a] (t)	Landed values ($000)	Average price to fishermen (¢/kg)
1966	30	—	30	2.4	8
1967	158	241	496	84	17
1968	3 939	713	5 029	1 005	20
1969	7 580	98	8 223	1 664	20
1970	5 634	90	7 534	1 582	21
1971	5 374	136	6 922	1 246	18
1972	5 392	51	6 718	1 948	29
1973	6 969	122	9 549	3 724	39
1974	6 704	217	10 046	3 817	38
1975	4 632	379	6 849	2 397	35
1976	7 568	489	10 500	4 619	44
1977	9 537	936	14 099	7 331	52
1978	10 462	3 189	21 936	12 503	57
1979	15 793	3 225	30 681	20 556	67
1980	14 854	2 500	28 539	16 838	59
1981	21 877	1 615	37 453	21 723	58
1982	31 585	2 190	47 004	43 243	92
1983	24 342	2 209	37 255	53 274	143

[a] Landings from Prince Edward Island, Quebec, New Brunswick, Newfoundland, Nova Scotia.

TABLE 2. Biomass and catch estimates (t) for the area 1, NW Cape Breton Island snow crab stock, 1977–83.

	1977	1978	1979	1980	1981	1982	1983
1) Biomass at start of season[a]		1827	1449	1418	1650	2132	1654
2) Growth and recruitment during season[a]		1189	790	420	40	0	0
3) Total exploitable biomass (1 + 2)[a]		3016	2239	1838	1690	2132	1654
4) Catch (logbook-derived) (Exploitation rate)	516	1941 (64%)	1391 (62%)	1105 (60%)	796 (47%)	953 (45%)	905 (55%)
5) Biomass at end of season (3–4)		1075	848	733	894	1179	749
6) Growth and recruitment between seasons		374	570	917	1238	475	
Management-imposed TAC:	—	—	1406	1224	1000	1000	1000

[a] Estimated by Leslie analyses of logbook data.

been allowed to take advantage of whatever production occurs from time to time. Seasonal landing patterns reflect the decay of the area 5 fishery since 1979 (Fig. 6).

Overall catch rates have progressively declined since 1978 with CPUE levels in 1983 being the lowest experienced in the area (Fig. 7). During the 1981, 1982, and 1983 fishing seasons catch rates remained at a depressed, relatively constant level that confounded Leslie analysis. Such CPUE patterns probably result from the collapsed nature of the stock and reflect the fishermen continually searching and moving their traps between fragmented, low-density snow crab "pockets." Hence, low catch rates were maintained even though commercial biomass was being progressively reduced (Fig. 8). The possibility that CPUE was being sustained by growth and recruitment equal in magnitude to the harvesting, was obviated by the dearth of newly molted crabs detected in commercial catch samples. The con-

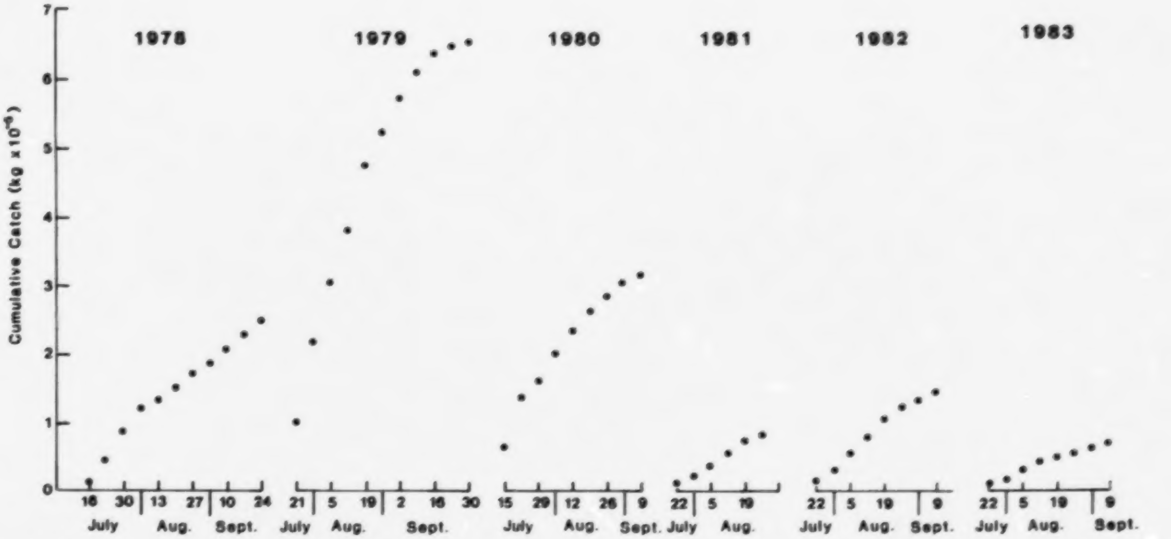

FIG. 6. Historical trends in cumulative snow crab landings, from logbook data, over time, for area 5, SE Cape Breton Island, 1978–83.

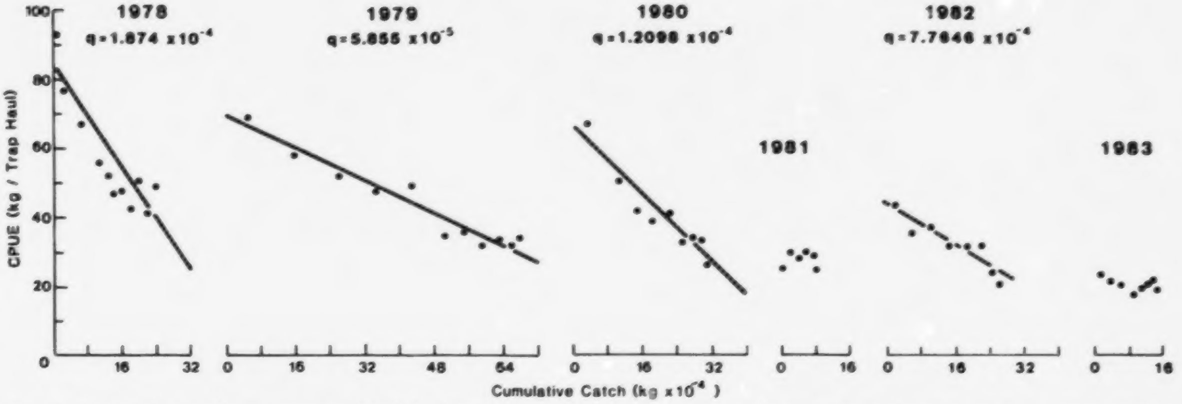

FIG. 7. Historical trends in mean weekly CPUE over cumulative snow crab landings, from logbook data, for area 5, SE Cape Breton Island, 1978–83. Note data points and regression lines used in Leslie analyses.

tinuing collapse of the area 5 snow crab resource as a result of failure of growth and recruitment to replace harvested biomass is detailed in Table 3.

DISCUSSION — CAPE BRETON ISLAND

The striking differences in the history of fisheries in area 1 and area 5 of Cape Breton Island appear remarkable given that the grounds are of approximately equal area, have similar numbers of fishermen and are separated by less than 160 km of landmass. As previously mentioned, the number of eggs being produced annually is assumed to be at pre-fishery levels, hence, recruit-overfishing and ensuing reproductive failures are unlikely to be a factor in the dynamics of the two stocks.

Management by stable-stock policy appears to have succeeded off the Gulf of St. Lawrence coast. Although exploitation in area 1 has been almost continuous since 1966, catch rates and commercial biomass have remained relatively stable since monitoring began in 1978. The magnitude of overall annual commercial biomass additions in area 1, despite being variable in periodicity, have appeared large and consistent. Such consistency in production has conferred stability and resilience to the stock, notwithstanding exploitation rates of 45–64%, and has facilitated management. Recent annual assessments (R. F. J. Bailey and R. J. Cormier, unpublished data) suggest that fishermen are not utilizing all of the snow crab grounds in area 1; if such is the case then the underexploited part of the stock may be acting as a further stabilizing buffer. Regardless, given that stability has been achieved in area 1 at the expense of curbing effort and landings, the long-term sustainable yield for the fishery appears to be at least 1000 t per annum.

When area 5 and adjacent Atlantic-coast snow crab grounds were opened to fishing in the late 1970's exploitation appears to have been based on accumulated virgin biomass. Although initial catch rates and landings were high, the commercial biomass in area 5 collapsed within three fishing seasons along with the snow crab

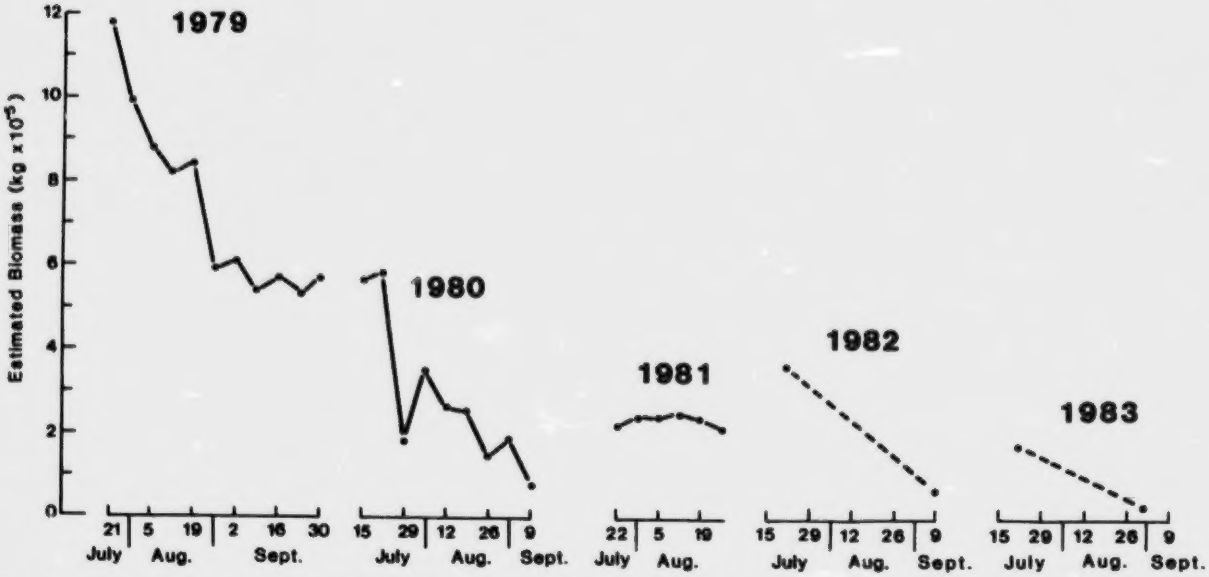

FIG. 8. Historical trends in estimated commercial biomass of snow crabs, derived from Leslie analyses of logbook data, over time, in area 5, SE Cape Breton Island, 1979–83. Note: The Leslie estimate of biomass in 1981 was generated using the 1980 value of q; the 1982 and 1983 biomass estimates are from Petersen analyses of tagging data.

TABLE 3. Biomass and catch estimates (t) for the area 5, SE Cape Breton Island snow crab stock, 1978–83.

	1978	1979	1980	1981	1982	1983
1) Biomass at start of season		1185[a]	543[a]	213[a]	357[b]	176[b]
2) Growth and recruitment during season		0	0	0	0	0
3) Total exploitable biomass (1 + 2)		1185	543	213	357	176
4) Catch (logbook-derived) (Exploitation rate)	250	683 (58%)	325 (60%)	82 (38%)	299 (84%)	149 (85%)
5) Biomass at end of season (3–4)		502	218	131	58	27
6) Growth and recruitment between seasons		41	-5	226	118	
Management-imposed TAC:			943	41	—	—

[a] Estimated by Leslie analyses of logbook data; the 1981 estimate was generated using the 1980 value for *q*.
[b] Estimated by Petersen analyses of tagging data.

fisheries in the remaining four Atlantic-coast areas. Possibly the Atlantic-coast areas around Cape Breton Island, being at the southern edge of known commercial snow crab concentrations in the Atlantic (Fig. 1) represent marginal grounds in terms of habitat. Although a review of biomass, growth and recruitment levels, as well as catch rates and size frequencies for area 5 reveals apparent recruitment failures, it may be that the situation represents the normal pattern of production. Alternatively, Davidson (1983) proposes that there is little endemic larval recruitment within the Atlantic coast of Cape Breton Island snow crab stocks. Larvae released from these stocks may become entrained in local gyres or swept northeast towards Newfoundland, but the predominant surface currents would tend to transport pelagic larvae south, down the coast of Nova Scotia or out into the Atlantic. Snow crab larvae are present on the Scotian Shelf and tend to be distributed with early larval stages in the north and later stages in the south (Roff et al. 1984). The larval distribution, plus the presence of small numbers of adult snow crab in the Bay of Fundy and Gulf of Maine, supports the concept of a large, southward loss of snow crab larvae from the Atlantic coast of Cape Breton Island. Both scenarios suggest that snow crab stocks around the Atlantic coast were probably established over time through small pulses of growth and larval recruitment. Such would account for the initially high catch rates and landings, the lack of resilience of the stocks to exploitation and the subsequent devastation of biomass and catch rates after only a few fishing seasons.

The future of the snow crab fishery off the Atlantic-coast of Cape Breton Island will depend on market demand and stock production patterns. With the current low catch rates, a decrease in the price paid to fishermen would make fishing uneconomical; on the other hand, prices notwithstanding, a continued lack of production will lead to the practical extinction of the resource.

The SW Gulf Experience

The history of the directed fishery for snow crab in the SW Gulf of St. Lawrence can be partitioned into three distinct phases: initially, a rapid exploration and development followed then by a period of adjustment for the industry, with relatively stable annual landings and, finally, a dramatic rise in annual landings (Table 1; Fig. 9). After an exploratory program in 1966, landings rose from 158 t in 1967 to 7580 t in 1969 as approximately 79 vessels from New Brunswick and Quebec became engaged in the fishery. Fishing grounds were rapidly expanded from Baie-des-Chaleurs towards the Magdalen Islands. The offshore gullies that are the source of most of the current landings were discovered as early as October 1968. The expansion of fishing activity did not immediately instigate a corresponding growth in the processing component of the industry. Although landings were generally stable over the period 1970–75 the relatively low prices paid to the fishermen had a strong influence on fishing effort (Table 1; Fig. 9). Prices have generally increased since 1976, mostly because of a heavy market demand for crab products created by the collapse of the Alaskan crab fisheries. From 1976 to 1982, annual landings increased dramatically with the record of 31 585 t set in 1982 representing a quadrupling of the 1969 level. However, recent annual landings have been adversely affected by high abundances of soft-shelled snow crabs during the summer months. After several failures to enforce a regulation prohibiting the landing of such crabs, the fishery was prematurely closed after mid-July of 1982 and 1983. Reopening the fishery in the fall of 1982 precipitated such a high fishing effort that it was not reopened in 1983.

Landing records are available from the beginning of the SW Gulf snow crab fishery although sampling of commercial catches has been carried out on a regular basis only since 1977. Similarly, logbook coverage since 1977 has been good, was limited during the period 1971–76, but considered good between 1968–70. Our appraisal of the snow crab fishery and stock dynamics in the southwestern Gulf is based on the various monitoring data since 1968 (Bailey 1978b; Lamoureux 1981; Lamoureux and Lafleur 1982; Bailey 1982; Bailey and Cormier 1983b, c).

The rise in CPUE (Fig. 9) until 1970 may be attributed to the exploitation of the accumulated virgin biomass and improvements in fishing techniques. From 1971 to 1976 CPUE values dropped markedly, presumably as the available fishing grounds became fully exploited and biomass was depleted. Although an increase in fishing effort, as evidenced from estimated total annual trap hauls (Fig. 9), has undoubtedly contributed to the rise in snow crab landings since 1977, there has also been a supporting increase in mean CPUE (Fig. 9). With exploitation rates, estimated by Leslie analyses, on the major fishing grounds remaining near 50–60%, the trend for increasing landings and CPUE since 1977 is attributed mainly to a substantial improvement in recruitment to the fishable stock. Unlike Cape Breton Island snow crab stocks, there are no reliable assessments of absolute snow crab biomass for the SW Gulf; however, the high incidence of newly molted crabs in recent years' catches support the relative abundance indices (CPUE and landings data) in inferring that there have been real increases in commercial biomass levels each year since 1977.

DISCUSSION — SW GULF OF ST. LAWRENCE

Based on an assessment of fishery data for 1966–77, Bailey (1978b) determined that exploitation rates had increased from 37% (1968) to 86% (1977) and, on the basis of yield : effort relationships, estimated by logistic and exponential surplus production models, suggested that the MSY for the SW Gulf was approximately 7000 t. However, with improvement in recruitment trends since 1977, assessments and yield projections based on data prior to 1977 have proved unrealistic. Presently, we have no indication of future recruitment trends or where the fishery will eventually stabilize.

There are two hypotheses which attempt to account for improvement in recruitment. Bailey (1982) proposed that Atlantic cod (*Gadus morhua*) biomass has a strong negative influence on snow crab recruitment to the fishery 3–6 yr later. The hypothesized mechanism is that cod, as a major predator, exerts a control over the numbers of pre-recruit snow crab in direct proportion to cod biomass. However, associated with a rise in cod biomass since the mid-1970's, the model predicted a reduction in snow crab landings beginning in 1982 when, in fact, record landings were achieved. Landings in 1983 dropped due to a premature closure of the fishery, but CPUE appears to have stabilized (Fig. 9). A declining trend in CPUE in the near future would tend to support the hypothesis for a cod control mechanism. Alternatively, Waiwood and Elner (1982) proposed that cod had not, hitherto, impacted the snow crab fishery and hypothesized that increased commercial harvesting of

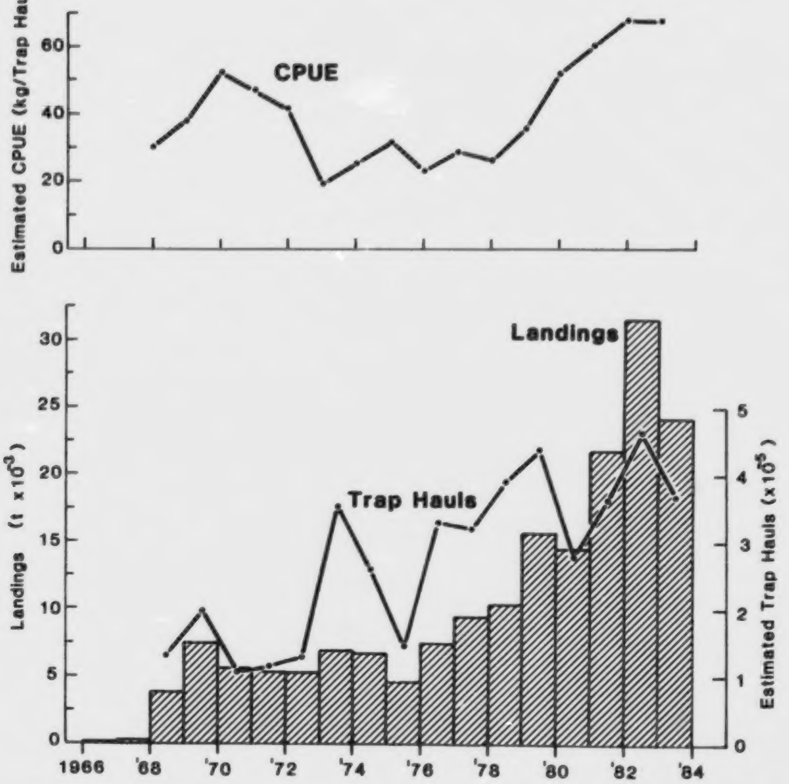

FIG. 9. Relationship between fishing effort, in terms of estimated total number of trap hauls for the combined Quebec and New Brunswick components of the fishing fleet, mean CPUE, from available logbook data for Quebec and New Brunswick vessels, and total snow crab landings from the SW Gulf of St. Lawrence, 1966–83.

crab was the mechanism driving the increased growth and recruitment phenomenon. The hypothesis states that prior to the fishery the SW Gulf snow crab stock was in a "saturated, stagnant" phase with larger, old crab monopolizing niche space and, by competition, restricting the resources available to smaller crabs on the commercial grounds. In such a situation, the growth and numbers of smaller crabs, upon which cod principally feed, would have been low and cod predation would have been limited (such is evidenced from cod stomach analyses prior to the snow crab fishery). However, once the fishery started to remove the older snow crabs and, hence, their inhibiting influence, the stock was released from a "stagnant" phase into a dynamic, high growth phase. The greater availability of resources on the commercial grounds led to increased growth and greater recruitment. Waiwood and Elner (1982) cite cod stomach analysis data as evidence that a switch in cod diet onto snow crab occurred at this time as larger numbers of small snow crabs and vulnerable, newly molted snow crabs became available. Waiwood and Elner's hypothesis would account for the increasing recruitment, CPUE and landings as greater numbers of snow crabs recruited onto the commercial grounds to fill the ecological "vacuums" created by the increasing fishing pressure. The proposed mechanism is similar to the theory for surplus production models. However, it differs from them in that the increase in annual production is so explosive that it allows the stock to exceed its virgin biomass level. The high exploitation rate drives the mechanism by generating a regular and critical drop in biomass; thus preventing competition by the recruited population from developing to restrict recruitment. The hypothesis implies that the maximum carrying capacity of the ecosystem is larger for the prerecruits than for the recruited population. However, the hypothesis does not predict at what point such a destabilized system will peak and its dynamics thereafter.

General Discussion

We have explored the dynamics of three Atlantic snow crab stocks under the same resource conservation regulations and similar resource allocation initiatives. After exploitation, commercial biomass trends have remained stable in one stock and demonstrated instability, in opposite directions, in the other two stocks. The critical determinant governing commercial biomass trends in all three situations is the dynamic relationship between annual production, in terms of growth and recruitment in the fishable stock, and annual yield. In NW Cape Breton Island, annual snow crab production has been consistent since 1977 and appears balanced by annual yield with the result that CPUE and commercial biomass trends have both remained stable. In contrast, in the SE Cape Breton Island snow crab stock, annual yields, although declining, have considerably exceeded annual production and resulted in the collapse of CPUE and commercial biomass. Yet again, in the SW Gulf of St. Lawrence, an enhanced production trend since 1977 has outpaced increases in effort and yield and led to increases in CPUE and commercial biomass. Although the dynamics of recruitment appear an indisputable cornerstone to effective stock management, it is difficult to envisage how such intelligence could have been discerned at the pre- or early-exploitation phases of the Atlantic snow crab fishery. Hindsight suggests that virgin biomass estimates could not have helped to elucidate stability or optimal yield. Indeed, given the scenario proposed by Waiwood and Elner (1982), if preliminary optimal yield projections for the SW Gulf fishery (Bailey 1978b) had been implemented into actual TAC's, the dynamics of the system may never have been shifted, the enhanced production trend may not have developed and the stock may have remained considerably underutilized. Similarly, the traditional method of approximating maximum sustainable yield (MSY) from the formulation:

(2) $\text{MSY} = 0.5MB_{o},$ (see Alverson and Pereyra 1969)

where M is the instantaneous rate of natural mortality and B_o is the estimated virgin biomass, may have underestimated potential yields from the SW Gulf and NW Cape Breton Island stocks while overestimating the potential of the SE Cape Breton Island stock.

What should management strategy be in the absence of assistance from effective non-equilibrium, predictive models? The dilemma is that there is a paradox between the need to predict production before achieving optimal yield and the present impossibility of predicting how exploitation will affect stock production without a long time-series of data collected during actual exploitation. If managers are too cautious in applying fishing pressure, data returns will be low and stocks may remain underutilized or not be shifted into a productive mode. Alternatively, even a conservative amount of fishing pressure could rapidly deplete a virgin stock with inherent poor production. Intuitively, a practical management approach is to recognize the present impossibility of predicting production dynamics under exploitation and allow the fishery itself to generate the required information, while at the same time attempting to minimize the risks from overfishing and overcapitalization. We suggest fishing pressure should first be applied at a moderate level, then built up only as production trends become evident from annual assessments. (These assessments should include prerecruit monitoring in order to predict fishing success 1–2 yr in advance.) Similar probing policies have been advocated by Walters and Hilborn (1976), Smith and Walters (1981) and Walters (1981). Ultimately, researchers should strive for long-term predictive models based on an understanding of the mechanisms controlling recruitment and, thus, provide managers the ideal basis for optimizing yields. Unfortunately, however, crab production dynamics appear particularly intractable and, as for the Atlantic snow crab, investigators have so far failed to elucidate the mechanisms responsible for regulating production in the unstable, male-only, Dungeness crab (*Cancer magister*), Tanner crab (*Chionoecetes bairdi*), and king crab (*Paralithodes camtschatica*) fisheries off the Pacific coast of North America (Colgate 1982; Methot and Botsford 1982).

At a meeting in 1969 to plan the early development of the Atlantic snow crab fishery, Davis (1969) recognized the "hazards of harvesting a hidden resource . . . whose response to our total fishing effort cannot be forecast with any degree of accuracy." At the same meeting, Smith (1969) argued for the expansion of the fishery to proceed slowly and stated that the important questions concerning the size of the resource was "not only how many animals are out there but also their production." He suggested that the question could only be answered by time and a fishery. Similarly, Wilder (1969) acknowledged the problem of imposing regulations that would restrict development of the fishery without proper knowledge on production levels. Evidently many problems debated at the 1969 meeting remained unresolved 15 yr onward.

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Yield Estimates for the New Zealand Rock Lobster Fishery

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ANNALA, J. H., AND D. B. ESTERMAN. 1986. Yield estimates for the New Zealand rock lobster fishery, p. 347–358. *In* G. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

The New Zealand rock lobster fishery became a controlled or limited entry fishery during 1980–81. The country was divided into 10 separate controlled fishery areas, and preliminary estimates of long-term sustainable yield were made for the entire fishery and for each area. These initial yield estimates have been revised based on additional data on the fishery. Catch and effort data were analyzed using a stock production model and other techniques. Maximum equilibrium yield for the North and South Islands combined (the Chatham Islands are considered separately) was estimated at 4700 t with effort equivalent to about 783 vessels or 45 680 vessel days fished. These are well within the range of past yield and effort figures. The estimate of long-term sustainable yield for the North and South Islands combined at the current level of effort was about 4200 t. Revised estimates of sustainable yield were also made for the 10 areas by apportioning the estimates of total yield on the basis of the average landings for the individual areas. The results from the various methods are compared and their application to the management of rock lobster fishery discussed.

En 1980–1981, la pêche de la langouste en Nouvelle-Zélande a fait l'objet d'un contrôle ou d'un accès limité pour la première fois. le pays a été divisé en 10 zones d'exploitation contrôlée et des estimations préliminaires du rendement soutenu à long terme ont été effectuées pour la pêche totale et pour chaque zone. Ces estimations initiales du rendement ont été révisées d'après des données supplémentaires sur la pêche et les données sur l'effort et les prises ont été analysées à l'aide d'un modèle de production d'un stock et d'autres techniques. Pour les îles du Nord et du Sud (les îles Chatham ne sont pas incluses), le rendement d'équilibre maximal s'élève à 4 700 t en présence d'un effort équivalent à environ 783 bateaux ou 45 680 jours-bateaux de pêche. Ceux-ci se situent dans la gamme des données antérieures sur le rendement et l'effort. Pour ce qui est des îles du Nord et du Sud combinées, l'estimation du rendement soutenu à long terme au niveau actuel d'effort s'élève à environ 4 200 t. On a aussi effectué des estimations révisées du rendement soutenu dans les 10 zones d'exploitation en répartissant par zone les estimations du rendement total en fonction des débarquements moyens. On compare les résultats obtenus à l'aide des diverses méthodes et on considère leurs applications à la gestion de la pêche de la langouste.

Introduction

The New Zealand rock lobster fishery is widespread. The main fishing grounds are on the north and east coasts of the North Island, and on the east, south, and southwest coasts of the South Island (including the waters around Stewart Island), and at the Chatham Islands (Fig. 1).

The main fishery is for the red or spiny rock lobster, *Jasus edwardsii*, which, since 1979, has accounted for at least 98% of the total landings. The fishery for the green or packhorse rock lobster, *J. verreauxi*, accounts for the rest.

The rock lobster fishery is the single most important inshore domestic fishery in New Zealand in terms of landed and export value and the number of vessels employed. In 1983, about 5000 t of rock lobsters were landed by 852 licensed vessels. More than 98% of the landings were taken by licensed pot fishermen, with the rest taken by licensed divers and as a by-catch from trawling and gill-netting. At an average ex-vessel value of about NZ$8.50/kg, this amounted to a landed value of about NZ$42 million. The export value totalled about NZ$51 million. Of the approximately 1400 full-time fishing vessels in the inshore fleet in 1983, about 800 were full-time rock lobster vessels (New Zealand Ministry of Agriculture and Fisheries, unpublished data).

The major regulations governing the rock lobster fishery include a minimum legal size of 152 mm tail length for both sexes (except in Otago where the size is 127 mm), a prohibition against taking berried females and soft-shelled animals, the requirement that all pots be fitted with escape gaps and a small number of closed areas. There is no closed season for rock lobsters, and no restrictions on pot numbers, size, or design, vessel characteristics, etc.

During 1980–81, the rock lobster fishery became a controlled or limited entry fishery. The country was divided into 10 separate controlled fishery areas (Fig. 1), and estimates were made of the long-term sustainable yield for the entire New Zealand fishery and for each area. These yield estimates were then combined with the results of a cost and earnings survey conducted by the New Zealand Fishing Industry Board to estimate the number of vessels that could economically fish each area. The number of vessels licensed for each area was greater than this number because a larger number of applicants met the entry criteria. Licences are non-transferable, and vessels cannot fish outside the area in which they are licensed.

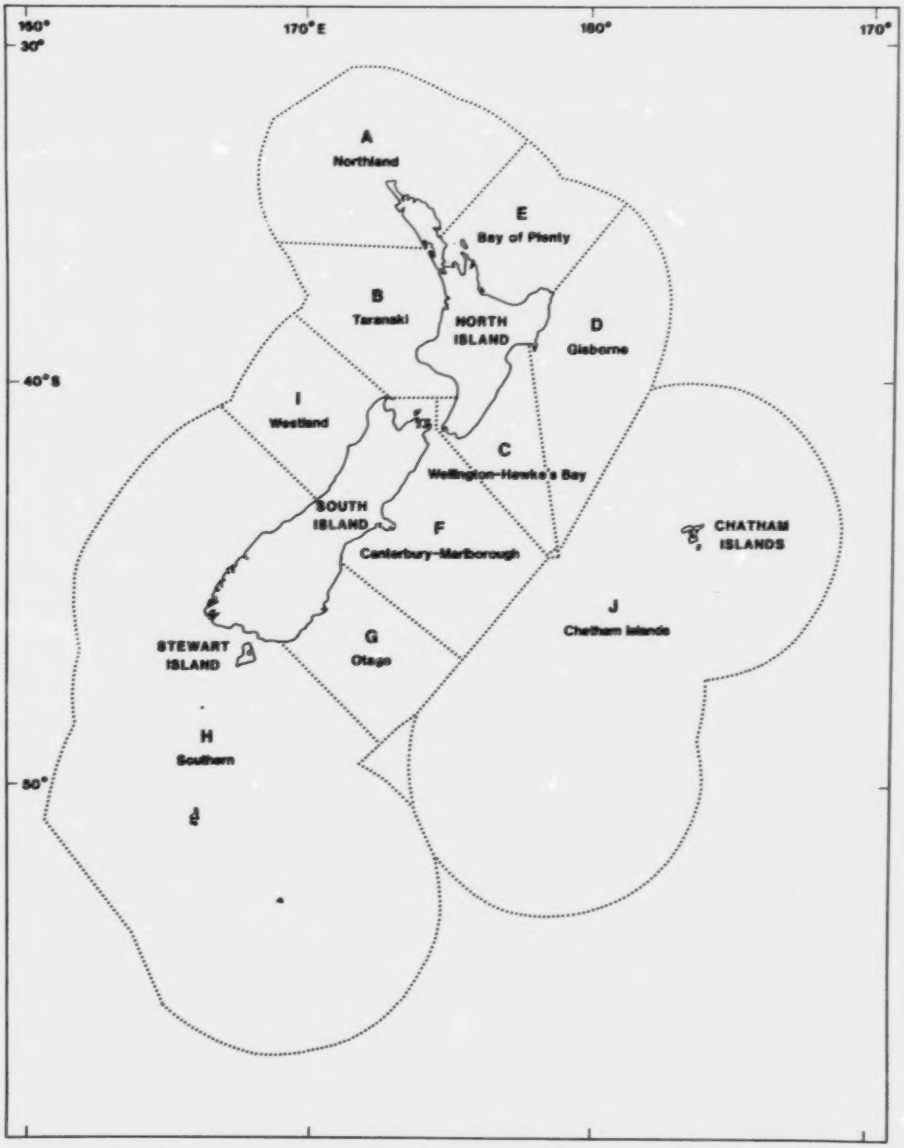
160°
30°
170° E
180°
170°
40° S
50°
A
Northland
E
Bay of Plenty
B
Taranaki
NORTH
ISLAND
D
Gisborne
I
Westland
C
Wellington–Hawke's Bay
SOUTH
ISLAND
F
Canterbury–Marlborough
CHATHAM
ISLANDS
J
Chatham Islands
STEWART
ISLAND
G
Otago
H
Southern

FIG. 1 Rock lobster controlled fishery areas.

In 1981, the Minister of Agriculture and Fisheries issued a policy statement which states in part: "The goal for the management of the fishery is to ensure a maximum continuing yield from the fishery taking into account the social and economic benefits for New Zealand and the fishing industry. Attainment of this goal involves (a) generally preventing any increase in fishing effort in the area fisheries; and (b) preparing the ground for an eventual reduction of fishing effort where such a reduction is necessary to maintain or increase yields and/or economic well-being". Current management policy is to reduce the number of licensed vessels towards the number that could economically fish each area as fishermen retire or leave the industry. (See Annala 1983a,b for a detailed description of the existing fishery regulations and the implementation of limited entry.)

The initial yield estimate of about 4200 t for the areas on the North and South Islands combined was made using the exponential stock production model of Fox (1970) with catch and effort data from 1945 to 1975 (Saila et al. 1979). The initial yield estimates for the individual areas were generally based on landings data from 1970 to 1978. However, a revised rock lobster fisheries statistics scheme was introduced in 1979 and has resulted in improved catch and effort data for the fishery.

The purpose of this paper is to describe and discuss revised estimates of long-term sustainable yield for the North and South Islands combined and for the individual areas. The implications of these revised estimates for the management of the fishery are then discussed.

Available Data

Catch and Effort Data – North and South Islands Combined

When making yield estimates for the rock lobster fishery, the areas on the North and South Islands combined are considered separately from the Chatham Islands. The areas have been separated because of the recent development of the fishery at the Chathams, which only began in 1965, and their geographical isolation, which has resulted in the Chathams being regarded for fisheries management purposes as a separate stock whose only connection with the mainland is probably via larval transport from the mainland.

Two sets of catch and effort data were used to estimate long-term sustainable yield for the North and South Islands combined. Only catch and effort data supplied by rock lobster fishermen using pots were analysed because of the small quantities taken by other methods. The analysis of catch and effort data can generally provide at best only a rough estimate of yield from a fishery. However, information on the population dynamics of the species which would permit more refined yield estimates is not available for most areas.

The first set of catch and effort data (Fig. 2) comprises total landings by the port of landing taken from fishing returns supplied by rock lobster fishermen using pots and the number of registered rock lobster potting vessels by port of registry as the measure of effort from 1945 to 1982 (Sanders 1983). Landings increased during the late 1940s and early 1950s as the fishery developed and expanded into previously unfished grounds. Landings peaked in the mid-1950s when all the main grounds had become exploited, decreased until the early 1960s, and have remained relatively stable since. The number of registered vessels increased steadily to reach a peak of 1903 in 1977 and then decreased to 815 in 1982. A number of fishermen left the fishery before the introduction of the controlled fishery in anticipation that they would not meet the entry requirements, and numbers have been further reduced since the fishery was controlled.

The number of registered rock lobster vessels is a very crude measure of effort, as the relationship between vessel numbers (nominal effort) and effective effort is unknown. The size and speed of a vessel, type of pot-hauling and fish-finding gear, and numbers and types and sizes of pots vary within and between areas, and all influence the effective effort exerted by a vessel (see Annala 1983b for details). However, this is the longest time series of catch and effort data available and provides at least a rough approximation of the catch–effort relationship in the fishery.

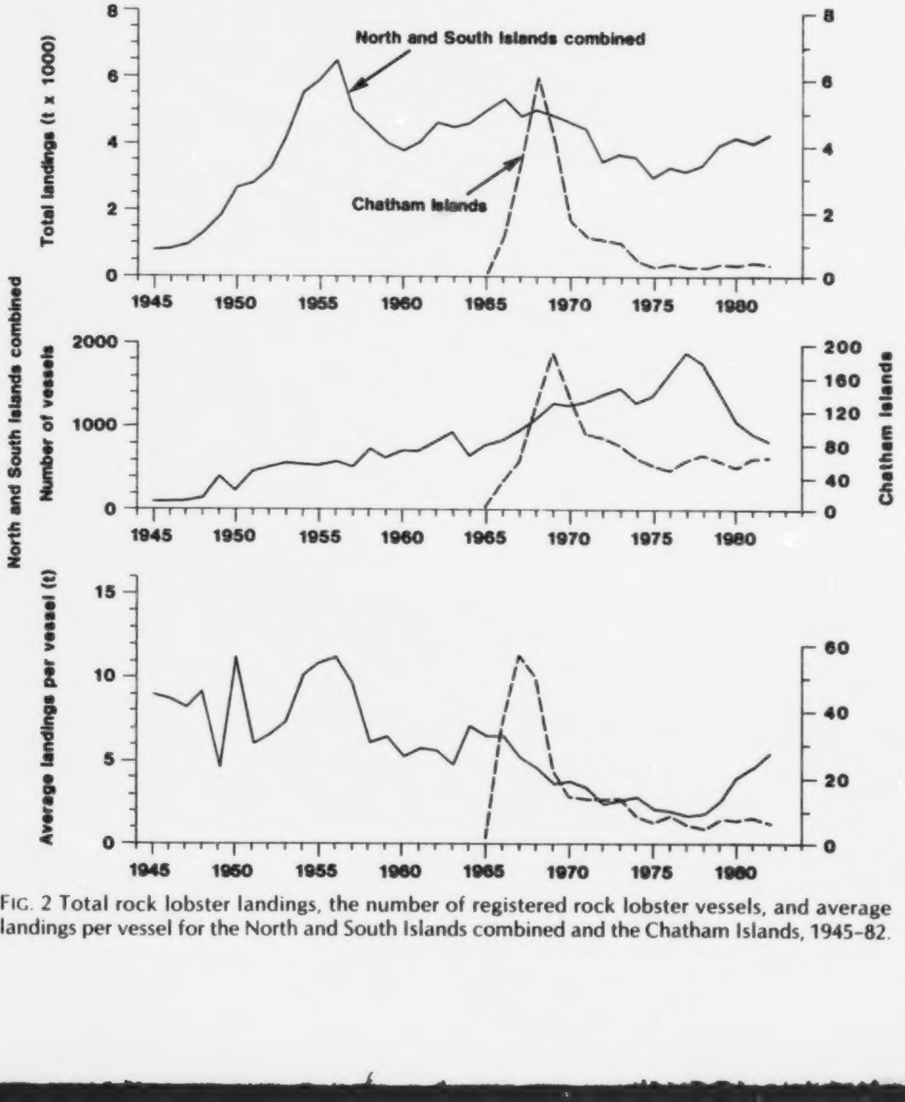

FIG. 2 Total rock lobster landings, the number of registered rock lobster vessels, and average landings per vessel for the North and South Islands combined and the Chatham Islands, 1945–82.

The second set of catch and effort figures provides data on the weight of rock lobsters caught and the number of vessel-days fished by area fished taken from fishing returns supplied by rock lobster fishermen using pots from 1963 to 1973 and 1979 to 1982 (Table 1, Fig. 3). These data were obtained from Fisheries Research Division Data Series publications on rock lobster fishery statistics and were not available when the initial yield estimates were made. The port of landing figures differed from the area fished figures, although generally not by a large amount, even though both sets of figures were taken from the fishing return forms. This difference occurred because some fishermen did not provide data on both the port of landing and area fished.

Catch and effort figures by area fished were not compiled during 1974–78, because of the collapse of the fisheries statistics scheme, but data were collected on the weight landed by port of landing. This required extrapolations to estimate the number of vessel-days fished. For the years 1963–73 and 1979–82 the estimated number of days fished were derived by dividing the total landings from the port of landing data by the average catch per day fished from the area fished data. The estimated number of days fished during 1968–73 and 1979–82 stabilized at between 70 000–80 000 days, so the number of days fished during 1974–78 was estimated by averaging the days fished during these two periods. This was considered a realistic assumption despite the increase in the number of registered vessels during 1974–78, as most of the new vessels were "part-timers" who only fished during a few months of the year (New Zealand Ministry of Agriculture and Fisheries, unpublished data).

The estimated number of days fished increased from about 41 000 in 1963 to about 81 000 in 1969 and then declined to about 70 000 in the early 1970s. Since 1979, the number of days fished has decreased from about 77 000 to about 69 000. The average catch per day fished declined from about 110 kg/day in 1963 to about 50 kg/day in 1972. Since 1979, the average catch per day fished increased from about 53 kg to 63 kg.

The number of vessel-days fished is also a rough measure of effective effort, as it does not take into account any changes in fishing power and catchability during the period. The number of pot-lifts may be a better measure of effective effort; however, data on the number of pots lifted each day are only available since 1979, and the time series is too short for any detailed analysis at this stage.

CATCH AND EFFORT DATA — INDIVIDUAL AREAS

Landings and effort data were also obtained for the seven major North and South Island areas and the Chatham Islands (Table 3). Data for Taranaki and Westland are not included because of the small size of these fisheries. The number of registered rock lobster vessels fishing in each area was not recorded before 1979 (except for the Chatham Islands), so the only data available are landings and the estimated number of days fished from 1963 to 1982. Because of the lack of catch and effort data by area fished during 1974–78, the port of landing figures were used for the entire 1963–82

TABLE 1. Landings, catch, effort, and catch per unit effort data for the North and South Islands combined, 1963–82, taken from fishing returns supplied by rock lobster fishermen using pots. See text for details.

Year	Catch[a] (t)	No. of days[b] fished	Average[a] catch per day fished (kg)	Landings[b] (t)	Estimated[c] No. of days fished
1963	4508	41 059	109.8	4554	41 478
1964	4483	46 631	96.1	4597	47 817
1965	4911	50 035	98.2	4984	50 779
1966	5526	57 565	96.0	5295	55 159
1967	4459	53 329	83.6	4782	57 192
1968	4492	65 132	69.0	4975	72 135
1969	4567	77 436	59.0	4768	80 844
1970	4627	70 969	65.2	4699	72 071
1971	4400	69 699	63.1	4478	70 935
1972	3450	70 261	49.1	3495	71 177
1973	3721	67 997	54.7	3748	68 490
1974				3643	72 242[d]
1975				2987	72 242[d]
1976				3311	72 242[d]
1977				3237	72 242[d]
1978				3418	72 242[d]
1979	3681	68 809	53.5	4156	77 688
1980	3995	68 459	58.4	4202	72 006
1981	3939	65 597	60.0	4083	67 995
1982	4231	67 025	63.1	4361	69 084

[a] Taken from area fished data

[b] Taken from port of landing data

[c] Estimated by dividing the landings figure by the average catch per day fished.

[d] Mean of the estimated No. of days fished during 1968–73 and 1979–82.

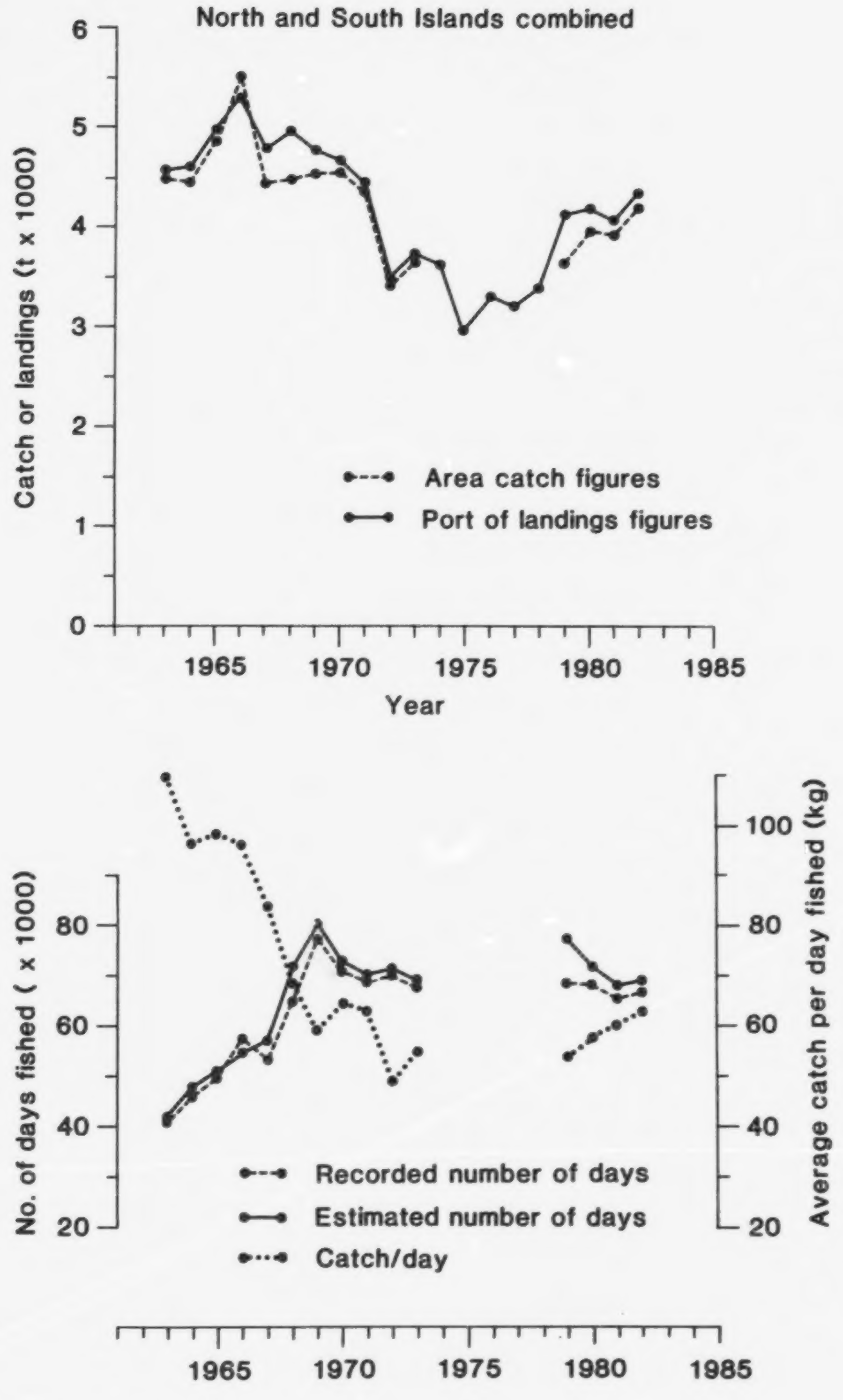

FIG. 3 Total rock lobster catch and landings, the number of recorded and estimated vessel-days fished, and the average catch per vessel-day fished for the North and South Islands combined, 1963–82.

period. All landings into the ports within the boundaries of a controlled fishery area were allocated to that area. Fishermen occasionally land rock lobsters into ports away from the area in which they fish. However, inspection of the data for 1963-73 and 1979-82, years when port of landing and area fished data were both available, revealed small differences between the two sets of figures for most years (the figures differed by <10% in 61% of the 105 comparisons).

The estimated number of days fished for each area for 1963-73 and 1979-82 was derived using the same method as for the North and South Islands combined. Even though the accuracy of the catch and effort data for the individual areas improved during 1979-82, the number of days fished was estimated from the port of landing figures to maintain consistency with the earlier data. The number of days fished during 1974-78 was estimated for each area using various assumptions based on the available information on the fishery and its catch and effort history.

Landings from all areas from Northland to Canterbury-Marlborough peaked during the late 1960s to early 1970s, declined through to the mid-1970s, and have increased since. The Otago and Southern areas have both experienced a general decline since the mid-1960s, although there have been larger year to year fluctuations than for the other areas. However, the decreased landings from Otago in 1972 and 1974 were partly the result of the size limit increases in those years (Annala 1977).

The fishery at the Chatham Islands did not begin until 1965, when one vessel landed 2 t of rock lobsters (Table 3, Fig. 2). It then developed very rapidly, with landings reaching a peak of 5958 t in 1968, and the number of vessels and days fished reaching their maximum in 1969. Landed weight, effort, and average landings per unit effort then declined rapidly. Since 1974, landings have fluctuated between about 300 and 500 t per year, the number of vessels from 45 to 65, and the estimated number of days fished from about 2500 to 4500.

Methods

The catch and effort data were analysed using two methods. First, a surplus yield or stock production model, Fox's (1975) equilibrium approximation approach to fitting the generalized stock production model, was used to estimate maximum equilibrium yield and optimum effort. Second, because total landings and the number of days fished have been relatively stable since the late 1960s, the data were averaged to estimate yield at the current level of effort.

The use of Fox's (1975) model requires that the following basic assumptions are met: (1) the model is applied to a closed, single unit population; (2) the population tends to a stable size and age distribution at each level of fishing effort; and (3) catchability remains constant. With regard to the first assumption, the available data suggest that rock lobsters around the North and South Islands probably come from one stock (Annala 1983b and references therein). However, the impact of fishing in one area on rock lobsters in widely separated areas is not known. The degree to which the second assumption has been met is unknown, although the average size (and presumably average age) of rock lobsters caught has declined considerably since the beginning of the fishery. As far as the third assumption is concerned, catchability has probably varied over the years because measures of nominal rather than effective effort have been used, and fishing power has increased with improvements in vessels and gear.

Results and Discussion

NORTH AND SOUTH ISLANDS COMBINED

Fox's (1975) model uses moving average values of fishing effort, the length of the moving average being the total number of years that a year class contributes significantly to the fishery. The number of significant year classes was estimated from size frequency data from the fishery and knowledge of its history (New Zealand Ministry of Agriculture and Fisheries, unpublished data). Various combinations of year classes based on these estimates were tested until the best fit, defined as the combination that maximizes the degree of fit index (R) of the model and minimizes the variability indices of the parameters, was achieved. For the landings-vessels data the best fit was obtained with 6 significant year classes in 1945 which decreased in a step-wise fashion to one significant year-class in 1978. This provided an estimate of maximum equilibrium yield of 4705 t with 783 vessels (Table 2a, Fig. 4a). For the landings-days data, the best estimate of maximum equilibrium yield of 4702 t with 45 680 days fished (Table 2a, Fig. 4b) was obtained with two significant year-classes in 1963 reducing to one year-class in 1974.

Using the second method (averaging the catch and effort data to estimate yield at the current level of effort), means were calculated for three groupings of years (Table 2b). In the first grouping, the analysis was extended back to 1963 because this was the earliest year for which data were available on the area fished and the number of days fished. In the second, the data from 1968 to 1982 were averaged because the estimated number of days fished had stabilized at between 70 000-80 000/year during this period. Both of these data sets were also averaged after excluding the data from 1974 to 1978, years during which landings were probably under-estimated due to the collapse of the fisheries statistics scheme. The third set includes only data from 1979 to 1982 from the new fisheries statistics scheme with its improved catch and effort information.

The average landings ranged from a low of 3971 ± 616 t (mean ± 1 standard deviation) for 1968-82, to a high of 4478 ± 483 t for 1963-73, 1979-82 (Table 2b). Because landings were probably under-estimated during 1974-78, the best estimates of yield at the current effort level of about 70 000 days fished are the average landings for 1968-73, 1979-82, and 1979-82 (about 4200-4300 t).

The estimates of maximum equilibrium yield obtained from Fox's (1975) model appear realistic and can be used as a guide in the management of the fishery. Landings have been stable in recent years, and the

TABLE 2. (a) Estimates of maximum equilibrium yield and optimum effort for the North and South Islands combined from Fox's (1975) model using the number of registered rock lobster vessels for 1945–82 and the number of vessel-days fished for 1963–82 as measures of effort.

Effort measure	Maximum equilibrium yield (t)	Optimum effort
Number of vessels	4 705	783 vessels
Number of vessel-days fished	4 702	45 680 days

TABLE 2. (b) Mean landings and mean estimated number of days fished (±1 standard deviation) for the North and South Islands combined for various combinations of years between 1963–82.

Years	Mean landings (t)	Mean No. of days fished
1963–73, 1979–82	4 478 ± 483	64 990 ± 11 594
1963–82	4 189 ± 670	—[a]
1968–73, 1979–82	4 296 ± 459	72 242 ± 4 064
1968–82	3 971 ± 616	—[a]
1979–82	4 200 ± 118	71 693 ± 4 341

[a] Not calculated because estimated number of days fished not available for 1974–78.

model estimates are within one standard deviation of most of the average landing values in Table 2b.

The model results, which suggest that a reduction in effort as measured by the number of vessels and days fished will result in an increase in yield of about 10% above the current level of 4200–4300 t, are supported by results from yield-per-recruit analyses. Analyses for various areas around New Zealand suggest that at the existing size limit a reduction in the instantaneous fishing mortality rate (F) from current estimated levels of 1.0 or greater to values of about 0.4 to 0.6 would result in an increase in yield-per-recruit of 0 to 15% (Saila et al. 1979, Annala, unpublished data).

The results of Fox's (1975) model using the number of registered vessels as the measure of effort suggest that the maximum equilibrium yield could be taken by 783 vessels (biological optimum). However, the estimates of optimum vessel numbers have been complicated by increases in the catchability of the average vessel in the fleet during recent years, especially since the mid-1970s. First, most of the vessels that entered the fishery during 1975–77 and that subsequently left the fishery during 1978–80, and which were removed during the initial round of licensing, were part-time rock lobster fishermen who fished a small number of days with few pots and caught small quantities of rock lobsters. Thus, the catchability of the average rock lobster vessel in 1982 was greater than the average vessel in 1977.

Second, the fishing power of the vessels remaining in the fishery has increased through improved fish-finding gear, increased pot numbers, improved pot design, etc. However, effective effort does not appear to have increased by the same proportion as nominal effort because of competition between units of gear. For example, in the Gisborne area, the average number of pot-lifts per vessel per day increased by about 40% between 1979 and 1982, while fishing mortality appears to have increased by less than 10% (Annala, unpublished data).

Therefore, it is unlikely that a reduction in vessel numbers to the predicted biological optimum of 783 as estimated from Fox's (1975) model would result in a significant reduction in effective effort and increased yields. The stated aim of the management policy is to reduce vessel numbers to the recommended number of 653 (the economic optimum), which is the sum of the recommended numbers for the individual areas (Annala 1983b). This latter figure may be closer to the biological optimum vessel number than the predicted value because the effort measure used is nominal rather than effective effort, and the catchability of the average vessel in the fleet has increased.

A similar situation pertains to the estimates of the optimum number of days fished. It is unlikely that a reduction in days to 45 680 as estimated from Fox's (1975) model would result in an increase in yield to the predicted maximum because of recent increases in fishing power. If the fishery was managed to improve yields by regulating the number of days fished, then further controls would be required to control fishing power and hence effective effort. At this stage there is no management plan in effect to manage the fishery to increase yields by reducing effective effort through controls on fishing power, number of days fished, etc. Even if such a plan was implemented, yields would not increase for several years.

Saila et al. (1979), using Fox's (1970) exponential stock production model with data on landings and the number of registered rock lobster vessels from 1945 to 1975, and with effort averaged over 3 years, estimated a maximum equilibrium yield of 4227 t with an optimum effort of 784 vessels. Anthony et al. (1986) have modified the Pella and Tomlinson (1969) generalized stock production model by incorporating a delay term to account for the lag between spawning and recruitment. Applying this model to the data on landings and the number of registered vessels for 1945–75 taken from Saila et al. (1979), they estimated a maximum equilibrium yield of about 4402 t and an optimum effort of about 773 vessels.

The estimates derived in this paper using Fox's (1975) model with the two data sets ending in 1982 are considered better estimates of maximum equilibrium yield and optimum effort than either of those based on the 1945 to 1975 catch and effort figures because the data sets ending in 1982 are more complete and extend over a longer period. Therefore, the best estimates of long-term sustainable yield for the North and South Islands combined range from a low of about 4200 t (based on average landings at current effort levels) to a high of about 4700 t (based on the stock production model results with a reduction in effort).

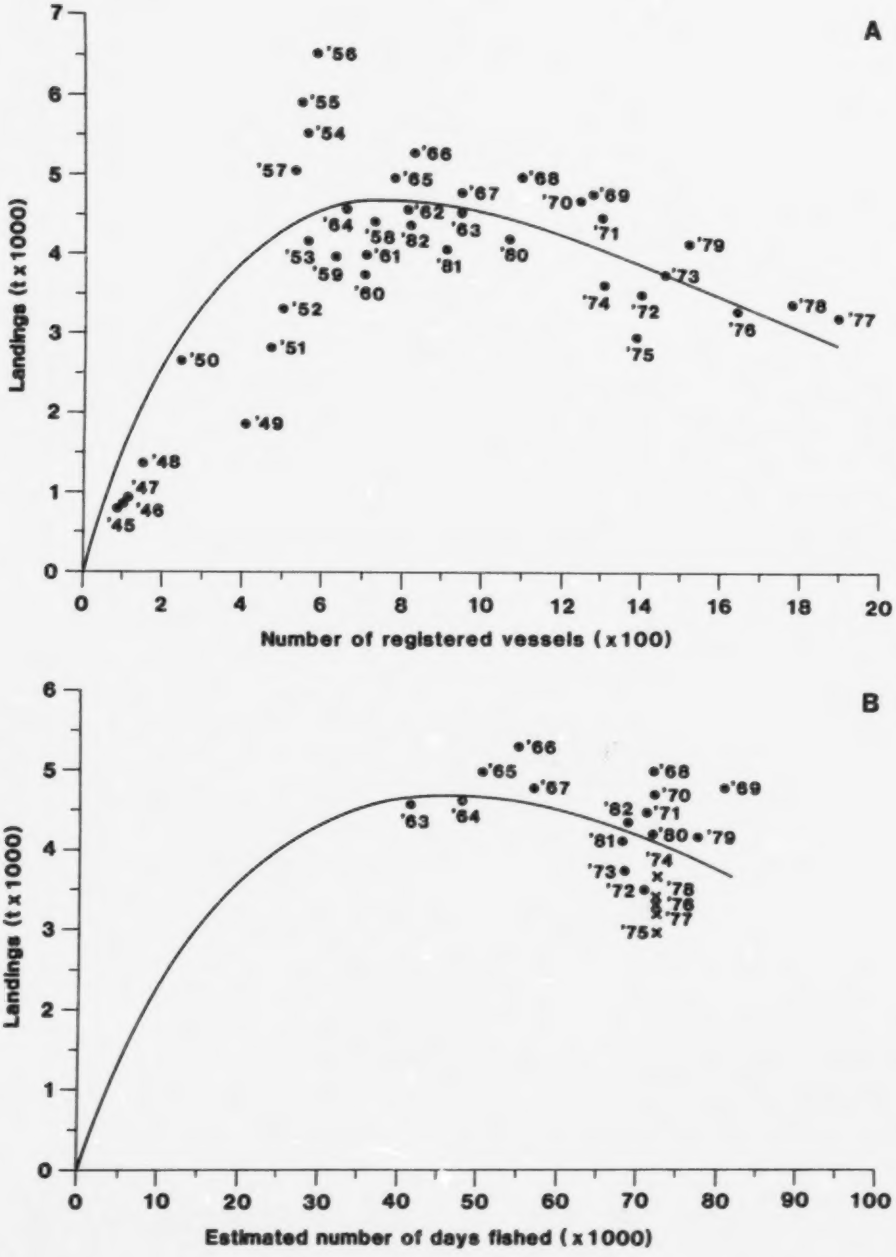

FIG. 4 Annual landings and effort ((A) number of registered rock lobster vessels for 1945–82 and (B) estimated number of vessel-days fished for 1963–82) data for the North and South Islands combined. Predicted equilibrium landings using Fox's equilibrium approximation approach to the generalized stock production model also shown. X's used for the landing-days data for 1974–78 to indicate these are average values for the number of vessel-days fished.

INDIVIDUAL AREAS

The number of licensed vessels is regulated separately for each of the 10 areas, so that the most important yield estimates for management purposes are those for each individual area.

Fox's (1975) model was applied to the data for the individual areas and various combinations of areas using combinations of significant year-classes of between 1 and 4 years. The model runs either failed to converge or gave unrealistic results, and the model was considered inappropriate for these data sets. Therefore, long-term sustainable yields were estimated by apportioning the estimates of total yield for the North and South Islands combined. Because of the lack of adequate information on rock lobster distribution, popu-

TABLE 3. Total landings from the port of landing figures and the estimated number of vessel-days fished for the 7 major areas on the North and South Islands and the Chatham Islands, 1963–82. See text for details (—, no data).

	Northland (A)		Wellington-Hawkes Bay (C)		Gisborne (D)		Bay of Plenty (E)	
Year	Landings (t)	Days fished	Landings (t)	Days fished	Landings (t)	Days fished	Landings (t)	Days fished
1963	108	2 534	378	5 640	112	1 233	251	6 595
1964	219	3 256	506	6 100	230	2 086	300	7 508
1965	249	2 889	616	5 360	213	2 736	290	7 824
1966	183	2 503	799	7 540	239	3 790	308	7 885
1967	149	2 726	537	6 033	385	5 343	344	8 186
1968	217	4 536	698	10 577	382	7 650	357	10 809
1969	338	8 230	729	12 353	244	5 817	314	13 096
1970	332	7 534	568	10 725	185	4 861	218	9 079
1971	337	6 282	419	8 911	144	4 494	193	7 736
1972	232	6 565	417	9 262	136	4 262	210	8 085
1973	77	3 951	388	8 809	116	3 323	184	7 646
1974	45	1 599	375	8 152	183	3 894	155	6 204
1975	78	2 144	404	8 414	162	3 115	138	5 520
1976	99	2 490	456	9 304	198	3 736	144	5 760
1977	182	3 853	438	8 580	220	4 583	199	7 968
1978	126	2 936	428	8 075	219	3 712	195	7 800
1979	106	3 588	625	11 358	306	5 098	285	10 973
1980	160	3 811	730	12 381	322	4 599	472	13 106
1981	193	3 307	775	12 300	327	4 538	442	13 403
1982	213	3 278	1 052	13 657	462	5 501	380	13 107

	Canterbury-Marlborough (F)		Otago (G)		Southern (H)		Chatham Islands (J)	
Year	Landings (t)	Days fished	Landings (t)	Days fished	Landings (t)	Days fished	Landings (t)	Days fished
1963	323	7 509	953	11 623	2 452	9 770	—	—
1964	448	7 597	595	8 879	2 271	13 203	—	—
1965	565	10 463	652	7 955	2 372	15 405	2	27
1966	663	11 436	766	6 492	2 315	15 967	1 271	1 439
1967	571	12 684	705	7 921	2 056	14 691	3 313	3 360
1968	535	15 283	849	7 715	1 880	16 640	5 958	9 548
1969	499	13 872	697	7 657	1 852	18 711	4 147	14 202
1970	445	12 038	722	9 139	2 230	19 560	1 751	10 180
1971	487	12 811	494	8 975	2 312	22 226	1 211	8 238
1972	470	13 429	250	6 950	1 743	22 940	1 088	6 217
1973	389	12 166	557	8 708	1 971	23 192	1 033	6 377
1974	316	8 778	391	5 013	1 533	17 621	518	4 125
1975	417	11 583	288	6 545	1 453	16 701	331	3 352
1976	382	10 611	262	6 238	1 680	19 310	391	2 750
1977	375	10 422	275	6 388	1 463	16 811	303	3 695
1978	342	9 513	422	7 673	1 635	18 793	293	4 468
1979	445	13 082	435	8 531	1 904	21 890	391	2 875
1980	490	10 654	319	6 648	1 642	18 654	342	2 542
1981	500	10 002	281	6 700	1 485	16 137	453	3 432
1982	591	11 373	142	5 079	1 458	15 850	415	3 921

lation abundance, effort distribution, and the area of fishable ground, yields were apportioned on the basis of the average landings for the individual areas (Table 4) instead of using data on effort or catch per unit effort.

The first column (Table 4) shows the original yield estimates made in 1979, which were based on landings for 1970–78. The chosen base year was 1970 because landings had stabilized from the peak values of the mid-1960s.

Average landings for 1979–82 are shown in the second column. For the major North Island areas and Canterbury–Marlborough, these figures were greater than the initial yield estimates. For the Otago and Southern areas, the 1979–82 landings were less than the initial yield estimates.

Average landings for 1970–82 are shown in the third column. These figures were greater than the initial yield estimates for the major North Island areas and Canterbury–Marlborough, about the same as the initial estimate for Otago, and slightly less than the initial estimate for Southern.

Average landings for 1963–82 are shown in the fourth

TABLE 4. Mean landings (±1 standard deviation) from the port of landing figures and estimates of long-term sustainable yield for the 10 controlled fishery areas, the North and South Islands combined, and the New Zealand totals. See text for further details.

Area		1979 yield estimate (t) (% of total)	1979–82 mean[a] landings (t) (% of total)	1970–82 mean[b] landings (t) (% of total)	1963–82 mean[b] landings (t) (% of total)	Estimated long-term yield (t)
Northland	(A)	120 (3.3%)	162 (3.9%)	168 ± 93 (4.4%)	182 ± 87 (4.3%)	185–200
Taranaki	(B)	45 (1.2%)	44 (1.1%)	45 ± 10 (1.2%)	41 ± 19 (1.0%)	40–45
Wellington-Hawkes Bay	(C)	375 (10.2%)	613 (14.9%)	404 (10.5%)[c]	416 (9.9%)[c]	415–465
Gisborne	(D)	350 (9.5%)	577 (14.0%)	379 (9.9%)[c]	392 (9.4%)[c]	395–445
Bay of Plenty	(E)	200 (5.4%)	358 (8.7%)	247 ± 113 (6.4%)	269 ± 97 (6.4%)	270–300
Canterbury-Marlborough	(F)	360 (9.8%)	484 (11.7%)	435 ± 75 (11.3%)	463 ± 94 (11.1%)	465–520
Otago	(G)	370 (10.1%)	276 (6.7%)	372 ± 154 (9.7%)	503 ± 230 (12.0%)	505–565
Southern	(H)	1800 (48.9%)	1572 (38.1%)	1731 ± 291 (45.1%)	1885 ± 344 (45.0%)	1885–2115
Westland	(I)	60 (1.6%)	40 (1.0%)	54 ± 16 (1.4%)[d]	41 ± 26 (1.0%)[d]	40–45
North & South Islands combined		3680 (100%)	4126 (100%)	3832 ± 534 (100%)	4189 ± 670 (100%)	4200–4700
Chatham Islands	(J)	350	399	655 ± 461	1284 ± 1583	400[e]
N.Z. Totals		4030	4584	4488 ± 870	5349 ± 1960	4600–5100

[a] Based on area figures.

[b] Based on port of landing figures.

[c] Landings for Wellington-Hawkes Bay and Gisborne apportioned on the basis of each area's portion of the total landings from the two areas combined during 1979–82.

[d] 1974–78 data missing.

[e] Based on average landings for 1974–82.

column. The time series was extended back to 1963 because landings increased during the late-1970s and early 1980s, and it appears that the fishery has recovered from the low landings experienced in the mid-1970s. These figures are greater than the initial estimates for all the major areas.

Estimates of long-term yield for the individual areas on the North and South Islands (column 5) were derived by partitioning the range of best estimates of total yield for the North and South Islands combined (4200–4700 t) by the percentage of the 1963–82 average landings contributed by each area. For example, for Northland 4.3% of 4200 t = 185 t and 4.3% of 4700 t = 200 t. Long-term yield for the Chatham Islands was estimated by averaging the landings for 1974–82, a period of relatively stable landings after the large initial peak in the late 1960s. The range of estimates in column 5 are the best estimates of yield that can be made at this stage.

The estimates of long-term yield for the individual areas are considered less accurate than the estimates for the North and South Islands combined. Landings from individual areas have fluctuated more widely than landings from the entire fishery. Larval settlement rates vary between areas, and this may affect subsequent recruitment into the fishery and landings (John Booth, pers. comm.). The use of long-term average landings as an estimate of yield is at best only a rough guide to what can be taken from each area and not a precise estimate of yield. However, despite the limitations on the data, the initial yield estimates were probably too low, and the revised estimates are considered more realistic.

The recommended vessel numbers for the individual areas should be re-assessed based on these revised yield estimates. However, economic conditions in the rock lobster fishery may have changed since the original economic survey was completed. Any changes to the recommended vessel numbers should be made only after the current economic conditions in the fishery are assessed through a revised cost and earnings survey or other means.

General Discussion

The rock lobster fishery on the North and South Islands combined appears to be an example of a steady or predictable fishery (Caddy and Gulland 1983) in which conditions change only slowly and landings remain at about the same level year after year. For such steady or stable fisheries, simple models may adequately explain the behaviour of the fishery. In the case of the rock lobster fishery, Fox's (1975) stock production model appears to give a reasonable approximation to conditions in the fishery and can provide a reasonable estimate of maximum equilibrium yield and optimum effort. The yield–effort curve is relatively flat, and the model results suggest that a reduction in effort below current levels would be required to increase yields from the current average of about 4200–4300 t to the predicted maximum equilibrium yield of 4700 t. However, without controls on the fishing power of the vessels in the fleet, effort would have to be reduced to levels below the predicted optimum values in order to maximise yield. Because there are currently no controls on effective effort, the best estimate of long-term yield under the existing management regime is the average of the landings at current effort levels.

Landings from the individual areas have fluctuated more widely, and when viewed separately give the impression of coming from cyclical or perhaps irregular stocks (Caddy and Gulland 1983). However, landings from the individual areas probably do not come from separate stocks, which highlights the importance of identifying stock boundaries before analysing catch and effort data. The reasons for the differences in landing trends are not known, but they are probably caused by environmental and biological factors which affect recruitment into the fishery.

If the fishery is managed to control effective effort in order to maximise yield, then the current management system based on individual areas should be re-examined. Because rock lobsters from individual areas do not come from separate stocks, it would be difficult to predict the level of effort required to maximise yield from a given area. The best management strategy in this case may be to remove the area restrictions to allow fishermen the right to fish wherever they choose and regulate effort on a New Zealand wide basis. On the other hand, it may be more appropriate to manage individual areas in a dynamic fashion, using short-term estimates of yield derived from predictive models based on catch and effort data, but incorporating environmental and biological factors, to determine optimum effort levels. This would allow the retention of area restrictions, which may be desirable for fisheries management and political purposes.

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CONTRIBUTED PAPERS

Recent Declines of Red King Crab (*Paralithodes camtschatica*) Populations and Reproductive Conditions Around the Kodiak Archipelago, Alaska

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The 1983 red king crab commercial fishery was closed completely around the Kodiak Archipelago for the first time since its initial development 33 years ago. Annual population surveys reveal current male and female king crab populations are at a 12 yr historic low level of abundance. Six consecutive years of below average recruitment of juvenile king crabs was the major contributor for the closure. Production of fertilized eggs, primarily due to low female population size, is at its lowest known level of 1.3 million eggs per pot lift and is expected to decline for at least the next 4 yr. Recruitment of crabs to legal size is also expected to be at historic low levels for at least the next 4 yr. A nemertean worm, *Carcinonemertes*, has recently been discovered to be an egg predator in red king crab clutches, significantly reducing reproductive output in some areas. Pacific cod has been shown to be an important predator on red king crabs during the crabs' molting period. The possible effects on king crab mortality by other known or suspected fish predators, commercial handling and diseases are also discussed.

En 1983, la pêche commerciale au crabe royal dans la région de l'archipel Kodiak a été totalement fermée pour la première fois depuis ses débuts, il y a 33 ans. Des dénombrements annuels ont montré que les populations actuelles de crabes royaux mâles et femelles avaient atteint leur niveau le plus bas en 12 ans. La fermeture est surtout due au fait que depuis six années consécutives, le recrutement des crabes royaux juvéniles est inférieur à la moyenne. Surtout parce que la population de femelles est faible, la production d'œufs fertilisés a atteint le niveau le plus bas connu, soit 1,3 million d'œufs par remontée de casier, et devrait diminuer encore durant les quatre prochaines années. On s'attend également à ce que, pour les quatre prochaines années au moins, le recrutement de crabes de taille réglementaire atteigne un minimum historique. On a constaté récemment qu'un ver némertien, *Carcinonemertes*, était un prédateur des paquets d'œufs de crabe royal, entraînant à certains endroits une diminution significative de la production de jeunes. On a montré que la morue du Pacifique est un important prédateur des crabes royaux durant leur période de mue. Les effets possibles, sur la mort du crabe royal, d'autres prédateurs connus ou potentiels, de la manutention et des maladies sont examinés ici.

Introduction

After 33 consecutive years of commercial fishing for red king crab (*Paralithodes camtschatica*) around the Kodiak Archipelago, a complete closure of the fishery was implemented during 1983 due to a depressed population level. This paper discusses: (1) changes in relative abundance and reproductive indices for red king crabs based on annual Alaska Department of Fish and Game (ADF&G) assessment surveys, and how this information relates to the fishery collapse; (2) future levels of reproductive output and recruitment of legal males; (3) the discovery of an undescribed nemertean worm, *Carcinonemertes* and its effect on clutch sizes of adult females in some areas; (4) king crab predation by Pacific cod and other possible fish predators during molting and non-molting periods and (5) mortality trends which may be due to handling or disease. Hereafter, the term king crab refers only to red king crab.

Methods and Materials

King and Tanner crab (*Chionoecetes bairdi*) population abundance surveys were conducted in waters of the Kodiak Archipelago, Alaska from 1972 to 1983. Surveys were conducted using crab pots between late June and early September with one to three vessels, each generally with four ADF&G technicians and four vessel crewmembers. Effort averaged 1 838 pots lifted per year, and ranged from 895 pots lifted in 1978, when only the southern half of the normal survey area was covered, to 2 391 pots in 1972. Usually 30 pots per day were fished while in bays and 40 pots per day were fished while in open ocean areas. The areal extent of the survey averaged about 18 500 km^2 between 1972–83. Approximately 95% of the historical king crab and 80% of the Tanner crab commercial catch came from within the survey area (Fig. 1). Commercial size pots measuring 203 × 203 × 76 cm, weighing 295 kg, with tunnel eye openings of 20 × 91 cm were used. Each pot was covered with 9 cm stretch mesh webbing rather than the 24 cm stretch mesh normally used in the commercial fishery. The smaller mesh size enabled retention of smaller crabs. Pots were baited with chopped frozen herring contained in two 0.95 L perforated bait jars. Pots were pulled daily, with soak times averaging 18–20 h except when weather or break periods prolonged fishing times. Catches of crabs were stand-

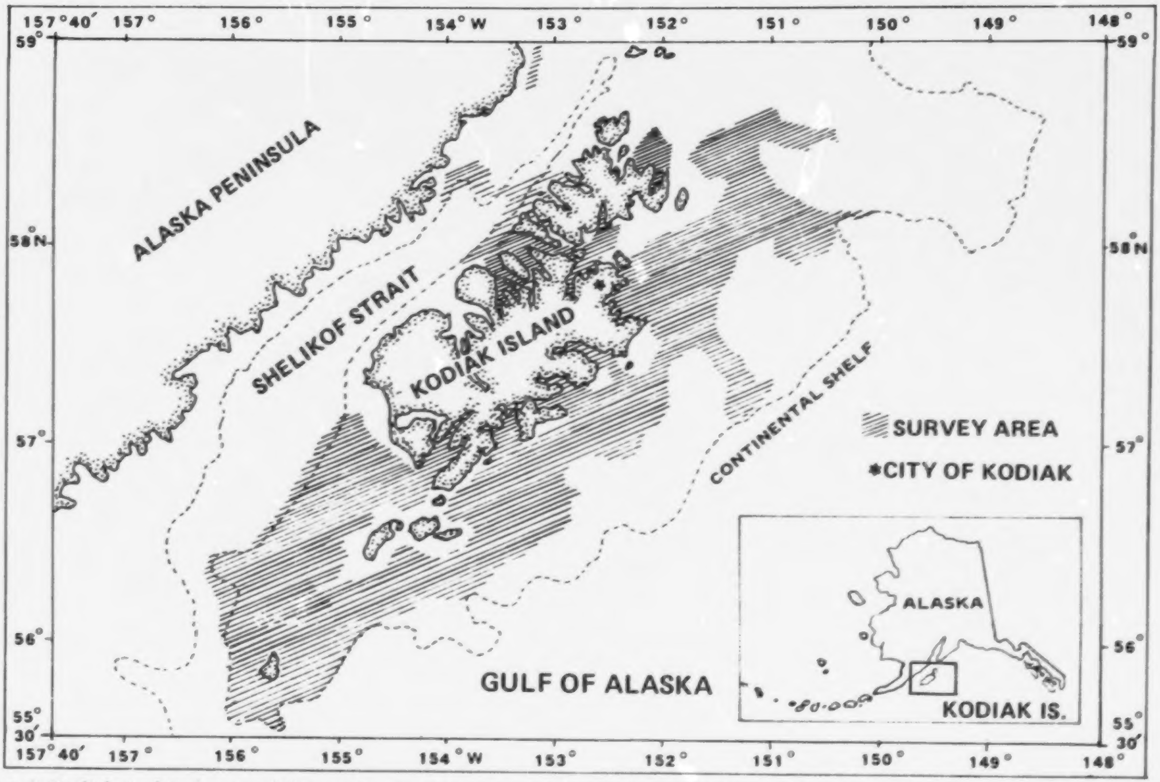


FIG. 1. Kodiak Archipelago and the maximum area surveyed during the 1972–83 annual crab population studies by the Alaska Department of Fish and Game.

ardized to a 24-h soak time based on the relationship established from 1964 to 1969 Kodiak commercial king crab logbook data (Rothschild et al. 1970).

Pots were set within stations generally running in a west to east direction. Stations were arranged in a systematic checkerboard grid pattern and no attempt was made to stratify by depth or bottom type. Station selections were based on known seasonal migrations, areas of commercial importance and survey catch performance. Bay stations usually consisted of three pots set 0.6 km apart, averaging one pot/4.3 km^2. Ocean stations were generally sampled with 10–13 pots spaced 0.5 km apart, averaging one pot/12.0 km^2. Approximately 15–20% of the survey effort was spent in bays and 80–85% in open ocean areas except in 1978 when no bays were fished. Depths at which pots were fished ranged between 7–289 m, however, 90% of pots were fished between 31–170 m.

Carapace length (CL) of king crabs and carapace width of Tanner crabs was measured with Vernier calipers to the nearest mm. Legal male crabs were tagged to estimate rates of fishing mortality, migration and growth. Subsampling of a particular group (e.g. adult females, legal or sublegal males) often occurred when catches exceeded 100 crabs/pot lift.

For computing adult king crab female/male sex ratios, all females with eggs and all females ≥ 116 mm CL without eggs were considered adults. Conversely, juveniles were defined as females without eggs ≤ 115 CL. Adult males were defined as males ≥ 91 mm CL (1972–79) and males ≥ 95 mm CL (1980–83). Small sexually mature males (< 110 mm CL) can mate in experimental conditions with larger females, but they are rarely observed to mate with females larger than themselves under natural conditions, which may be due to competition from larger males (Powell et al. 1973). Inclusion of smaller sexually mature males into the adult female/male ratio in this paper, probably underestimates the sex ratio which occurs in the breeding population.

Egg clutch size for each adult female king crab measured was estimated and recorded as a percent of the maximum volume of eggs that a female could hold. All eggs were assumed to be fertilized since unmated adult females which do not resorb their eggs generally lose them within 100 d of extrusion (McMullen and Yoshihara 1969). A random sample of 670 females during the 1983 survey also revealed no unfertilized eggs (Powell and Blau 1984). Egg clutches observed on surveys are generally 3–5 mo into the 11–12 mo brooding period. The percent clutch size for each adult female observed on each survey was multiplied by the number of eggs contained in a full (100%) clutch for that size female based on a regression of the number of eggs in full clutches over various carapace lengths (Haynes 1968). Total number of eggs from all females sampled on each survey was then summed. This procedure was necessary because the total number of eggs carried by full clutch females can vary by a factor of three and one half over the observed size range of mature Gulf of

Alaska female king crab. Egg abundance from each survey was divided by the number of pots fished to give an annual index of the number of eggs/pot, the measure of reproductive output for the population.

The fourth pleopod and attached eggs from both select and randomly chosen females were sampled in 1983 and 1984 crab surveys to determine presence of egg predators. Samples of live females were shipped to the University of Alaska for studies involving behavior of egg predators and samples of pleopods were shipped to the University of California to determine incidence of egg clutch inhabitants and egg mortalities.

Three additional surveys were conducted in 1984. In February 1984, 6 mo after the 1983 annual summer crab survey, three bays and one ocean area were resurveyed to determine if clutch size of female king crab had changed; egg samples from each of these bays contained *Carcinonemertes* the previous summer. A total of 85 pots were lifted. Not all summer stations were resampled in the winter survey due to shorter days and weather constraints (i.e. 36 pot lifts/day in summer versus 15 pot lifts/day in winter), and stations were selected based on where the majority of females were caught in summer. To date only summer and winter samples from Kiliuda and Alitak bays have been analyzed with the χ^2 statistic. A second survey was conducted April 16–19, when 11 tows were made using a 400 eastern otter trawl on Long Island Bank, 28–46 km east of the City of Kodiak, to look for recently molted king crabs in stomachs of predatory fish. A third survey was conducted June 6–10, to study distribution of crabs and clutch condition of females in three bays on the northeastern side of Kodiak Island.

Fork lengths of Pacific cod (*Gadus macrocephalus*) and Pacific halibut (*Hippoglossus stenolepis*) caught in pots were measured to the nearest cm. Examination of cod stomach contents occurred as time permitted. Other incidentally caught fish and invertebrates were enumerated and recorded.

Results and Discussion

During the 1972–83 period approximately one million king crab, one quarter million Tanner crabs and 54 000 fish were caught during annual ADF&G crab population survey (Table 1). This survey effort represents approximately 16 continuous man years of shipboard work (based on an 8-h work day), 660 d (1.8 yr) of fishing, 44 000 km of travel and 22 000 pot lifts. King and Tanner crab fisheries in the Kodiak area during the 1972–83 period were the second most valuable crab fisheries in Alaska, after the Bristol Bay king and Tanner crab fisheries.

RELATIVE ABUNDANCE OF KING CRABS

Within the last 7 yr (1977–83) of the 12 yr of surveys, there has been a tenfold decrease in total survey catch of king crabs from 160 000 to 16 200 animals (Fig. 2). Highest catch of juvenile females, sublegal males and total crabs occurred in 1977. Conversely, the lowest catch of juvenile and adult females, legal males and total crab was in 1983. Lowest abundance of sublegal crabs was in 1982 and highest abundance for legal males was in 1974. Highest relative abundance of adult females occurred in 1978, the year after the peak in juvenile abundance.

Abundance of crabs as indexed by CPUE (catch/pot) from year to year is consistent with observed patterns of recruitment, natural mortality, and fishing mortality. Trackability of length frequency modes for female and male king crabs has been excellent from these annual surveys. Annual growth of cohorts and shifts in length frequency modes can be easily followed (Fig. 2). Catchability of small crabs generally increases for their first 3 yr of susceptibility to the gear. The large increase in abundance of juvenile females and sublegal males from 1975 to 1978 is considered largely due to increased catchability (Fig. 2). Tracking of length frequency modes for legal males is more complex because of increasing skipmolting with increasing size and variable fishing mortality rates.

IRREGULAR RECRUITMENT OF JUVENILES

Irregular recruitment has occurred with Kodiak king crab during the survey period. Survey catches of the smallest juvenile crab cohorts (about 4 yr old) available to the sampling gear indicate only two periods of above-average abundance, 1972 and 1975–77. These cohorts dominated the populations in the ensuing years. Relative strengths of these cohorts are most discernible in survey catches of juvenile females (Fig. 2). Six consecutive years of below-average catches of juvenile crabs began in 1978 (Fig. 2). Lowest abundance of newly recruited legal male crabs (148–164 mm CL) occurred in 1982 and 1983 and was a result of low recruitment of juveniles in 1978 and 1979.

REPRODUCTIVE CONDITION

Egg Output — Output of eggs is the most accurate survey index of the overall reproductive condition of the population. Egg output has ranged from 5.0 million eggs/pot lift in 1974 to a low of 1.3 in 1983 (Fig. 2). During the 12-yr survey period the average number of eggs/adult female has varied by nearly a factor of two from 113 000 in 1978 to 221 000 in 1975. Mean catch/pot of adult females has ranged fourfold from six in 1983 to 27 in 1978 (Fig. 2). The most important variable contributing to the eggs/pot index has been number of females captured, not average number of eggs/female.

Sex Ratios — Male king crabs of varying sizes and shell ages can mate successfully (producing fertilized clutches of ≥ 75%) with four to nine females under experimental conditions. However, factors such as timing of molting, size difference of adults and spatial distribution may be more important than just relative sex ratio in determining mating success (Powell et al. 1974). Adult female/male sex ratios during the survey period ranged from 0.32 in 1975 to 2.16 in 1983 and progressively increased during this 9-yr period (Fig. 2). This imbalance causes concern that a lack of males may be contributing to partial fertilization and reduced clutch size.

TABLE 1. Cumulative catches of red king and Tanner crabs, Pacific cod and halibut made during 12 annual Kodiak crab surveys 1972–83, and the commercial catch and ex-vessel value of king and Tanner crabs harvested during this period.

	Females		Males		
Species	Number	%	Number	%	Totals
Red king crab[a]	430 000	45%	527 000	55%	957 000
Tanner crab[a]	27 000	10%	233 000	90%	260 000
Pacific cod[b]					46 000
Pacific halibut[b]					8 000

	Commercial Harvest			
	Metric Tons		Ex-Vessel Value ($U.S. millions)	
	Total	Per Year	Total	Per Year
Red king crab	86 000	7 000	$220	$18
Tanner crab	12 000	1 000	$138	$11

[a] Crab catches standardized to a 1-day period.
[b] Fish catches are actual, non-standardized.

For at least 3 to 4 yr following maturation, the instantaneous mortality rates for female red king crab in the Bering Sea are substantially higher than rates for males (Reeves and Marasco 1980). Natural mortality rates for Kodiak adult female king crab have not been adequately studied. If Kodiak female king crab mortality rates are analogous to those in the Bering Sea, then this may partially explain why with a males only commercial fishery, females have not substantially outnumbered males in the early years of annual surveys.

For the next 4 yr (1984–87) reproductive output (millions of eggs/pot) is expected to decline dramatically. The 1982 and 1983 surveys produced historic low numbers of juvenile males and females indicating it will be at least three more years before a strong recruitment of juvenile females could mature to a size that would substantially increase reproductive output over current record low levels. In 1983, 50% of adult females caught on the surveys were 10 yr or older. The relative scarcity of females 12 yr old (approximately 135 mm) indicates that natural mortality takes a major toll before crabs attain this age/size (Fig. 2). A progressive loss of the major portion of the 1983 adult female population is predicted to occur within the next few years.

If good recruitment of juveniles does not materialize in 1985 or 1986 from the relatively high egg outputs of 1980 and 1981, then future recruitment must come from the lowest observed egg production, beginning in 1983 (Fig. 2). Because of an 8–10 yr time lag between mating of the spawning population and subsequent recruitment to legal size, the 12 yr of survey data yields only five spawner-recruit points. This is too short a time series to allow determination of a stock-recruitment relationship.

Egg Predator — Carcinonemertes, a genus of nemertean worms, has been known for over a century. This genus is composed of species living as epibionts on various brachyuran crabs. One species, *C. errans*, was recently confirmed as an egg predator of its host the Dungeness crab (*Cancer magister*) (Wickham 1978, 1980). In June of 1984, for the first time in an anomuran crab, an undescribed species of *Carcinonemertes*, was shown to eat the eggs of red king crabs from which they were collected (A. J. Paul, pers. comm.). The crabs were from Uganik Bay, Kodiak Island.

The fourth pleopod and attached eggs from 15 different ovigerous king crab were collected. Four of these crabs were from Viekoda Bay, Kodiak Island and 11 were from Kachemak Bay, near the city of Homer, 210 km northeast of the city of Kodiak. Analysis of the 15 egg samples revealed a density of 17.5 worms/1 000 crab eggs with an average egg mortality of 70.5%. This analysis was based on number of empty egg cases and dead eggs assumed to have been caused by *Carcinonemertes*. These worm densities and egg mortalities are similar to epidemic levels observed over the past 10 yr on the central California coast for *C. errans* on Dungeness crabs (Wickham 1979a).

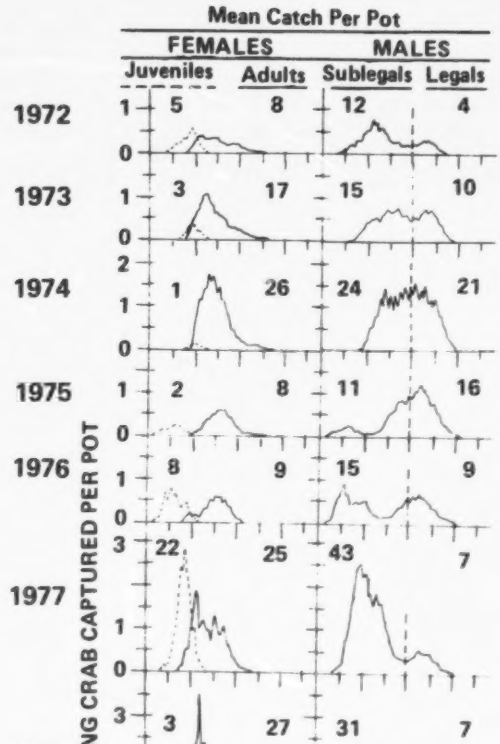
The ADF&G in conjunction with University of California investigators began a distributional study of *Carcinonemertes* in king crag egg clutches in 1983. To date over 300 pleopod samples have been collected from southeast Alaska to Norton Sound; approximately 150 have been collected from the Kodiak area. Preliminary examination of these samples indicates a widespread distribution of *Carcinonemertes* in red king crab from Southeast Alaska to the Aleutian Islands with at least two different undescribed species present (D. E. Wickham, pers. comm.). In addition I observed *Carcinonemertes* in egg clutches of approximately ten Tanner crabs around Kodiak Island.

Replicate sampling of female king crabs and egg clutches was carried out in Kiliuda and Alitak bays on the 1983 annual Kodiak survey and during a special 1984 winter resurvey. Of the four areas resurveyed, these two bays provided the largest winter samples and are the only two areas whose data have been analyzed to date.

Summer and winter samples from Kiliuda and Alitak bays are assumed to be from the same respective populations, since replicate samples were taken from the same locations and their respective age-size frequencies showed no major discrepancies (Fig. 3). No recently molted females were observed in the winter survey and hence no shell growth occurred during this period.

Changes in clutch size over time was based on analysis of 125–145 mm, and 114–141 mm, groups of female crab in Kiliuda and Alitak bays, respectively. These size ranges constitute 90% of crabs measured in summer and winter and correspond to approximate age groups of 10–14 yr and 8–13 yr, respectively. Frequency distributions of clutch sizes for the two bays in the summer were not significantly different ($\alpha = 0.1$). Clutch sizes of these female crabs appear to be relatively consistent in summer and provide a sound basis for quantifying clutch size changes.

Clutch sizes observed in winter samples were compared to summer sizes for each bay. In both bays, there was a significant difference ($\alpha = 0.1$) in clutch size between summer and winter. A shift from a high to a lower overall clutch size, for size classes analyzed,



	Mean Catch Per Pot				Total Crab		Sex Ratio of	Eggs Per Pot
	FEMALES		MALES		Mean Per Pot - Number		Adults (♀/♂)	(Millions)
	Juveniles	Adults	Sublegals	Legals				
1972	5	8	12	4	29	67,100	0.57	1.8
1973	3	17	15	10	45	89,300	0.67	3.3
1974	1	26	24	21	72	144,600	0.58	5.0
1975	2	8	11	16	37	69,500	0.32	1.8
1976	8	9	15	9	41	80,700	0.54	1.7
1977	22	25	43	7	97	160,500	0.55	4.0
1978	3	27	31	7	68	59,700	0.73	3.0
1979	1	21	17	9	48	81,500	0.83	3.3
1980	1	22	14	8	45	104,800	1.05	4.1
1981	1	18	8	9	36	64,300	1.11	3.3
1982	< 1	7	2	2	11	19,200	1.63	1.4
1983	< 1	6	3	< 1	9	16,200	2.16	1.3
OVERALL MEAN					43	79,800	0.70	2.8

FIG. 2. Length frequencies, relative abundance and reproductive conditions found during annual Kodiak crab population surveys, 1972–83, by the Alaska Department of Fish and Game. The vertical dashed line at 145 mm (148 mm since 1981) converts to 178 mm (7 in) carapace width, the minimum legal size limit.

occurred between summer and winter samplings (Fig. 4). Decline in clutch size occurred across all size classes and was not attributable to a major change in any one size-class. By using midpoints of the clutch size percent-fullness categories, the overall change in percent fullness of clutches can be computed. Overall percent fullness of egg clutches in Kiliuda Bay decreased from 82% in summer to 55% in winter. Similarly, the overall per-

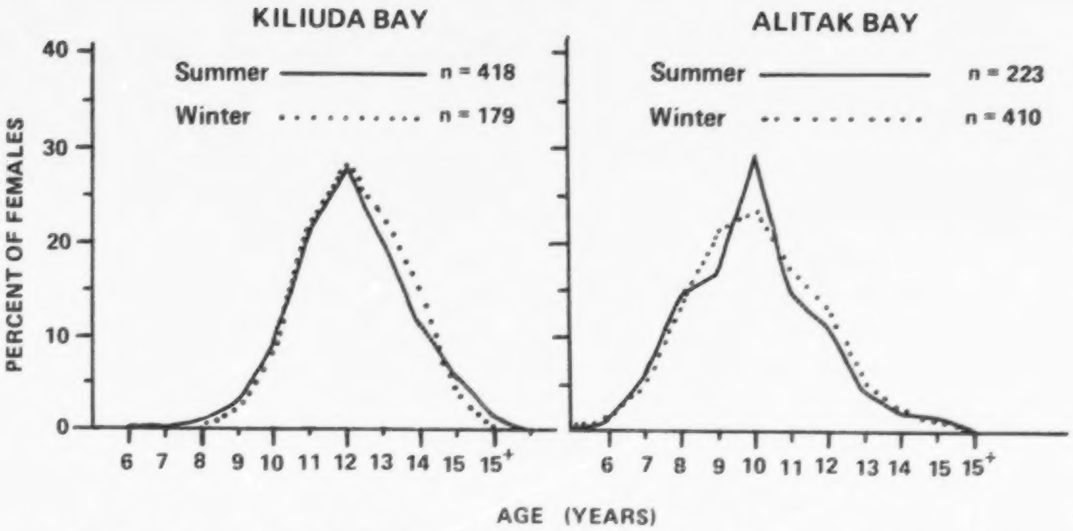


FIG. 3. Comparison of the percent age classes of female red king crab populations captured in the summer (August 1983) and winter (February 1984) on replicate surveys in Kiliuda and Alitak bays, Kodiak Island, Alaska. Age classes are approximate but assigned to the following carapace length groups (mm): 6 yr = 102–107, 7 yr = 108–113, 8 yr = 114–119, 9 yr = 120–124, 10 yr = 125–129, 11 yr = 130–133, 12 yr = 134–137, 13 yr = 142–145, 15 yr = 146–149, 15 + yr = 150 +.

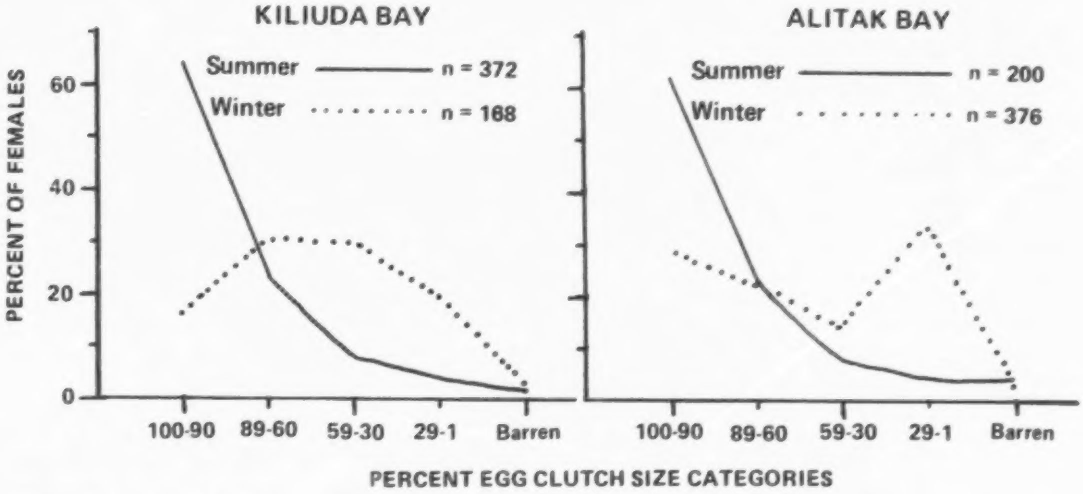


FIG. 4. Decrease in egg clutch size for female red king crabs sampled in summer (August 1983) and winter (February 1984) in Kiliuda and Alitak bays, Kodiak Island, Alaska. Overall decrease in ovigerity by 33 and 32% in each respective bay is attributed to the nemertean egg predator *Carcinonemertes* sp.

cent fullness of egg clutches in Alitak Bay decreased from 80% in the summer to 55% in winter. These reductions in clutch size are believed to be due to the egg predator *Carcinonemertes*.

In early September during the 1983 annual survey, all adult females caught in Uganik Bay ($n = 341$) were barren, having only empty egg cases attached to the pleopods. This marked the first time in the 30 yr history of Kodiak king crab research that a population of females around the archipelago was found totally barren. *Carcinonemertes* was the major suspect for egg loss in Uganik Bay but this was not corroborated. In early June 1984 of the subsequent reproductive year, crabs from Uganik Bay were again sampled on a special ADF&G survey. Clutches from this sampling contained *Carcinonemertes* and averaged only 34% of the maximum clutch size potential. Overall mean density of nemertean worms was 20.4 per 100 eggs (SD = 11) (A. J. Paul, pers. comm.). This mean nemertean density was 8 to 115 times greater than observed for *C. errans* in Dungeness crab egg clutches (Wickham 1979a). When placed in test tubes with eggs from the same king crab clutch they lived in, *Carcinonemertes* was observed to eat the eggs (A. J. Paul, pers. comm.). Overall occurrence of empty egg shells was 80% (SD = 24) and overall number of dead eggs was 6% (SD = 2). The complete reproductive failure in 1983 for females sampled in Uganik Bay was likely due to the egg predator *Carcino-*

nemertes, and egg clutches were almost completely decimated after only 5 mo into the normal 11-12 mo brooding period.

Carcinonemertes is strongly suspected to have also reduced egg clutches of female king crab in three bays around Kodiak Island, and in Kachemak Bay on the mainland. *Carcinonemertes* has been observed in other bays and offshore areas around Kodiak Island but the extent of its distribution and abundance is unknown. The eggs/pot index (Fig. 2) must be considered an overestimate of yearly reproductive output of the population because the index does not take into account progressive egg loss due to predation by *Carcinonemertes* or other factors. To account for progressive egg loss in king crabs and reproductive index accuracy, females should be sampled closer to the time of egg hatching.

Increases in *C. errans* during a period of record low levels of Dungeness crab abundance has led to the hypothesis that when the host population sharply declines the density of worms/female increases, thereby reducing the fecundity to a level which might prevent or delay recovery of the crab population from low levels. This may explain why the central California Dungeness crab fishery collapsed and has not yet recovered (Wickham 1979a,b). A similar situation may be occurring in localized areas within the Kodiak Archipelago. Abundance of king crabs in the last 12 yr has decreased tenfold since 1977, perhaps leaving remaining females with inflated densities of *Carcinonemertes*.

COD PREDATION ON RED KING CRAB

During the 12 yr of annual crab surveys around Kodiak 46 125 Pacific cod (*Gadus macrocephalus*) were captured, ranging from 0.5/pot in 1972 to 5.7/pot in 1983. Stomach contents of 27% ($n = 12\ 443$) of these cod were examined. Only 77 (0.6%) fish contained king crab, some of which may have been consumed while they were in the pots. The only thorough food habits analysis from ADF&G surveys was by Jewett (1978) who examined 3 933 cod stomachs between 1973-75. Fish, Tanner crab and shrimp, in decreasing order of occurrence, were the most frequently consumed prey. This trend is believed to be similar for all survey years. The same order of frequency was found for the most important food items in a 1977 southeastern Alaska summer study of 590 cod; no king crab tissues were found (Clausen 1981). Analysis of 455 Pacific cod stomachs from three separate summer trawl surveys conducted in Pavlof Bay, on the south side of the Alaska Peninsula, in 1980 and 1981 by ADF&G and the U.S. National Marine Fishery Service (NMFS) showed pink shrimp, euphausids, walleye pollock and capelin to be the most frequent prey. Little evidence for cod preying on king crab was found as only one stomach contained king crab parts (Albers and Anderson 1985).

Two cod predation studies were undertaken during the main adult king crab molting season. Each study used a 400 mesh eastern otter trawl as the sampling gear. The first study conducted in 1981 by NMFS in the eastern Bering Sea found that 9.8% of cod had whole or parts of king crabs in their stomachs (Table 2). Seventy-five percent of the ingested king crab by weight were taken from cod sampled during May 23-31, 1981, when crab were soft from recent molting (June 1985). The second study was conducted April 16-19, 1984 by ADF&G. In this study trawling occurred on a portion of Long Island Bank, a known king crab molting and breeding area (McMullen 1967). Softshell and premolt adult female king crabs were observed in the catch. Of the Pacific cod sampled, 10.9% contained king crab parts. In the NMFS study no crabs were believed ingested while in the trawl and any cod with fish or other food hanging out of or in the mouths were excluded from the study (June 1985). In the ADF&G study only one cod with a king crab leg sticking out of the mouth was included in the findings. Lengths of cod consuming king crab were similar for both NMFS and ADF&G studies, ranging between 41-79 cm (Table 2). If only the number of cod within the length range which consumed king crab are considered, the percentage of cod ingesting king crab rises to 13.8% and 13.1% in the NMFS and ADF&G studies, respectively. Based on these studies the rate of consumption of king crab by Pacific cod is 16-18 times higher during the molting season compared to the summer non-molting period. The amount of king crab consumed by cod may be higher during the first few days after the crabs' molting period prior to hardening of the exoskeleton.

Pacific cod in the eastern Bering Sea move to shallower inshore waters in spring once temperatures rise above 2°C (A. Shimada, pers. comm.). Their distribution overlaps that of king crab during the general adult molting period. In the eastern Bering Sea, an estimated 6.6 million (7 380 t) king crabs were consumed during their 1981 molting season by 235 800 t of Pacific cod (June 1985). This explains approximately 25% of the estimated decrease in number of nonlegal king crab caught with otter trawls between 1980 and 1981 (June 1985).

Abundance of Pacific cod in the eastern Bering Sea from 1978 to 1983 increased from 0.3 to 1.1 million t (Bakkala and Wespestad 1984). There are no abundance estimates for cod which include the Kodiak area surveyed for crab. Yet like the Bering Sea, cod abundance quadrupled between 1978 and 1983 using the Kodiak survey catch per pot of cod as an indicator. Kodiak and Bering Sea crab survey catches of cod reached historic peak abundances in 1983. In surveys since 1978, the 1977 year class of Pacific cod was the dominant in the Bering Sea and Gulf of Alaska (Owen and Blackburn 1983; Bakkala and Wespestad 1984). In Kodiak, the cod abundance index from 1978 to 1983 crab surveys increased as abundance of king crabs coincidentally decreased.

Besides Pacific cod, a number of other groundfish species such as Pacific halibut, walleye pollock (*Theragra chalcogramma*), yellowfin sole (*Limanda aspera*) and sculpins (*Myoxocephalus* and *Hemilepidotus*) are known or suspected predators of king crab (Smith and Walters 1982). The groundfish community as a whole, especially roundfish (Pacific cod and walleye pollock), flatfish and cottids apparently increased substantially throughout much of the Gulf of Alaska between 1961 and the mid-1970's (Ronholt et al. 1978). Incidental

TABLE 2. Comparison of the catch of Pacific cod and their ingestion of red king crab from trawl studies conducted by National Marine Fisheries Service (May-June 1981) and the Alaska Department of Fish and Game (April 1984).

	May-June 1981	April 1984
Comparison of Overall Cod Samples		
No. cod stomachs examined	864	404
No. ♂ cod and percent	395 (46%)	230 (57%)
No. ♀ cod and percent	469 (54%)	172 (43%)
Mean length (cm)	49.7 (total length)	52.7 (fork length)
Length range (cm)	12-89 (total length)	34-84 (fork length)
Depth range fished (m)	13-155	60-144
Comparison of Cod Which Contained King Crab		
No. of cod with king crab	85 (9.8%)	44 (10.9%)
No. ♂ cod and percent	37 (44%)	24 (56%)
No. ♀ cod and percent	48 (56%)	20 (44%)
Mean length (cm)	57.7 (total length)	56.5 (fork length)
Length range (cm)	41-78 (total length)	45-79 (fork length)
Depth range (m)	9-97	60-144
No. of cod which ate king crab vs. No. of cod within the same length range	85 of 615 (13.8%)	44 of 339 (13.1%)
No. whole crab	34	none
King crab size (mm CL)	80-130	—

catch rates of groundfish as a whole have also increased and remained high from the mid-1970's to the present on Kodiak ADF&G shrimp trawl surveys (Watson and Thompson 1984). Walleye pollock, for example, has been a major component of the ADF&G shrimp survey groundfish catch and the 1975-79 year classes of pollock were strong (Alton and Rose 1985). Although pollock are not a confirmed predator of king crab, a major part of their diet, particularly of 1-2 yr olds, consists of small planktonic crustaceans (Smith and Walters 1982). Pacific halibut is a known predator of softshell king crab (Gray 1964; Blackburn and Blau 1985). The incidental catch of halibut has increased since 1978 on annual Kodiak crab surveys (Powell and Blau 1984). International Pacific Halibut Commission (IPHC) juvenile halibut survey catch rates in the Gulf of Alaska have been increasing since the mid-1970's, reaching peaks in 1980 and 1981 (IPHC 1983), and legal size halibut abundance in the Kodiak area increased from 1978 through 1982.

OTHER MORTALITY FACTORS

There have been two substantial, unexplained declines in overall abundance of king crab across most size classes during the 12 yr history of annual surveys. The largest declines occurred from 1974 to 1975 and from 1981 to 1982 when overall mean catch/pot of king crab dropped 49% and 69%, respectively (Fig. 2). Between 1974-75 and 1981-82, female and male CPUE declined 63 and 40%, and 68 and 82%, respectively. These declines appear partly attributable to below average recruitment of juveniles, commercial harvest of males, mortality of older females, predation by fish, commercial handling of nonlegal crab and disease.

Comprehensive studies to assess commercial handling mortality of discarded nonlegal size king crabs have not been undertaken. No apparent relationship exists between the number of commercial pot lifts and the subsequent change in the overall non-legal population level. Commercial effort which has increased progressively from 71 000 pot lifts in 1972 to 389 000 pot lifts in 1981 (ADF&G 1983). The greatest level of commercial effort occurred in 1981, followed by the largest overall mean catch/pot decline in 1982. In 1974 110 000 commercial pots were lifted, the third lowest in the 1972-83 period, yet the second largest overall king crab population decline occurred in the following year's survey (Fig. 2). During 1982, 284 000 pots were lifted, yet the change in overall crab abundance between 1982 and 1983 was relatively small.

Since 1982, 260 red, blue (*Paralithodes platypus*) and brown (*Lithodes aequispina*) king crab have been examined histopathologically for disease organisms. Of these, 28 crabs (10.8%) were infected by viruses and 11 (4.2%) were infected by microsporidian protozoans. Both diseases are suspected to be highly lethal (A. Sparks, pers. comm.).

Summary and Conclusions

Twelve years (1972-83) of red king crab survey data from waters around the Kodiak Archipelago reveal irregular recruitment of juvenile crabs (4 yr old). Six consecutive years of below average recruitment of juvenile crabs occurred from 1978 to 1983. Major causes of poor recruitment are unknown but high mortality occurred somewhere from the egg to the 4 yr old juvenile stage.

Commercial overfishing of king crab populations is often the first explanation proposed for fishery crashes.

Commercial harvests removed a large volume (86 000 t) of legal males over 12 yr, averaging 38% of the estimated standing stock during the span of the surveys (Blau 1985). Additional but unquantified losses of various size classes of crabs may have occurred from commercial handling and lost pots.

Since 1978 natural mortality loss of adults has been far greater than gain from recruitment to the adult population. Initial studies suggest that Pacific cod could be a significant predator on king crab during the molting period and may have played an important role in the overall decline of Kodiak king crab stocks. Since 1978, cod abundance has increased to historic highs. Perhaps more importantly, the groundfish community as a whole has increased in abundance during the decade prior to the present decline and has remained high since 1978. Known and suspected king crab predators which are a part of the groundfish community have likely preyed on king crabs of all ages. The recent discovery of both apparently highly lethal diseases and the egg predator *Carcinonemertes* also seem important.

Four more years of depressed legal male abundance are predicted from the record low 1983 sublegal population. If depressed levels of juvenile crabs continue for three or more years, then depressed levels of egg production may delay rebuilding of the Kodiak red king crab stocks back up to their average 1973–81 population levels for 10 yr or more.

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Recruitment Variability of Juvenile Red King Crab, *Paralithodes camtschatica*, in the Southeastern Bering Sea[1]

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Size (carapace length)–frequency data from trawl surveys of red king crab (*Paralithodes camtschatica*) in the southeastern Bering Sea were examined for size-class modes of juveniles. These modes were compared to results of previously published growth models to determine the youngest age-class consistently caught in sampling gear. Consistency was judged on the basis of both number of positive samples and variability in number of individuals per sample. Most crabs younger than four years old were caught at comparatively few stations, sometimes in large numbers and usually at geographically scattered sites. These large but relatively rare catches are interpreted as encounters with podding, or at least highly aggregated, individuals. Crabs corresponding in size to 4-yr-olds (4's) were widely distributed, however, and in some years occurred in great abundance. These crabs apparently are caught in lower proportion to their abundance than older (larger) crabs, but the survey data appear reliable enough to use in formulating an index of year-class strength. The index consists of a population estimate of crabs within a narrow size range selected to encompass the mode of greatest abundance of a year-class. A fixed (a priori) definition of the appropriate index size for 4-yr-old crabs did not focus ideally on the actual modes of abundance of strong year-classes seen in these data. Modes of apparent 4's occurred at a size somewhat smaller than predicted, but moving the indexing size range downward to provide a better visual fit to the size-frequency data did not qualitatively alter results. The index of abundance of 4-yr-olds for the time series dating 1969–83 identifies two large year-classes, 1971 and 1978. These large year-classes were produced by two opposite extremes of stock size. Their fates by the time they reached harvestable size also were contrary, as one contributed to the largest harvests on record while the other was reduced to extremely low abundance before it reached legal size. Demise of the latter year-class paralleled a dramatic decline in the stock as a whole.

Les données de fréquence de taille (longueur de la carapace) obtenues par dénombrement au chalut du crabe royal (*Paralithodes camtschatica*) de la partie sud-est de la mer de Béring ont fait l'objet d'un examen portant sur les classes modales de la taille des juvéniles. Ces modes ont été comparés aux résultats de modèles de croissance décrits dans les publications afin de déterminer la plus jeune classe d'âge régulièrement capturée à l'aide des engins d'échantillonnage. Cette régularité a été déterminée à partir du nombre d'échantillons positifs et de la variabilité du nombre d'individus par échantillon. La majorité des crabes de moins de 4 ans étaient capturés à un nombre relativement faible de stations, parfois en nombre important mais généralement en des lieux dispersés. Il semble que ces prises importantes, mais relativement rares, correspondaient à des « bancs » ou à de fortes concentrations d'individus. Les crabes de même taille que les individus de 4 ans présentaient une large distribution et étaient très abondants au cours de certaines années. Il semble que ces crabes soient capturés en plus faibles proportions que les crabes plus vieux (plus gros) si l'on se base sur leur abondance, mais les données des relevés sont suffisamment fiables pour permettre la détermination d'un indice d'importance de la classe annuelle. Cet indice est une estimation de la population des crabes à l'intérieur d'une gamme étroite de tailles choisie de façon à recouper le mode de plus grande abondance de la classe annuelle. Une définition fixe (a priori) de l'indice de taille approprié pour les crabes de 4 ans ne recoupe pas parfaitement les modes réels d'abondance des fortes classes annuelles indiquées par les données. Les modes des individus de 4 ans (âge apparent) étaient notés pour des individus d'une taille légèrement inférieure à celle prévue, mais le déplacement vers le bas de la gamme servant à déterminer l'indice de taille, effectué de façon à obtenir un meilleur ajustement visuel aux données de fréquences de

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taille, n'avait pas d'effet qualitatif sur les résultats. L'indice d'abondance des individus de 4 ans appliqué aux séries chronologiques de 1969 à 1983 a permis de déterminer deux importantes classes annuelles : l'une en 1971 et l'autre en 1978. Ces deux importantes classes annuelles étaient le produit de deux tailles de stocks extrêmes et opposées. Elles ont aussi donné des résultats opposés quand elles ont atteint la taille commerciale; l'une a été à l'origine d'une des plus importantes récoltes jamais effectuées tandis que l'autre présentait un niveau d'abondance extrêmement faible avant d'atteindre la taille légale. La disparition de cette dernière classe annuelle a correspondu à un déclin extrêmement important de l'ensemble du stock.

Introduction

Major fisheries for red king crab (*Paralithodes camtschatica*, Tilesius) have existed in Alaskan waters since the 1950's (Otto 1981). The fishery is for male crabs only, which reach legal size [135 mm carapace length (CL)] mostly during their eighth year, though entry to the fishery may occur from 7 to 10 yr of age (Balsiger 1974). The southeastern Bering Sea, Kodiak Island, and eastern Aleutian Islands have been major producing areas. Statewide harvest of this species peaked in 1980 at 80 136 metric tonnes (t) with approximately 74% of this coming from the southeastern Bering Sea. The previous peak in harvest from this region occurred in 1964, when an estimated 29 024 t was taken by foreign fishing operations. Both peaks in landings followed apparent peaks in abundance of exploitable (legal-sized male) crabs, as indicated by catch per unit effort data of foreign fisheries prior to 1965 and by U.S. trawl surveys since 1968 (Hayes 1983). Standard trawl surveys conducted annually in the southeastern Bering Sea since 1969 show dramatic changes in abundance of exploitable red king crabs (Fig. 1).

The primary objective of this investigation was to use the trawl data base to examine interannual variability in abundance of year-classes of juvenile crabs. We then examined the relationship between year-class abundance and parental female spawning stock; and that between year-class abundance and subsequent harvestable stock. In order to do this, it was necessary to select an age-class which could be reliably identified in the survey data. We sought the youngest age-class possible for this purpose for two reasons. First, the youngest crabs were expected to show the least size overlap between neighboring year-classes (Weber 1967; McCaughran and Powell 1977) and therefore should be the least ambiguous to identify. Second, we wanted to be able to identify year-classes as close to the year of origin as possible. Previous papers have discussed fluctuations in stocks of red king crabs from the southeastern Bering Sea (Otto 1981; Hayes 1983), but have not attempted to quantify differences between various year-classes.

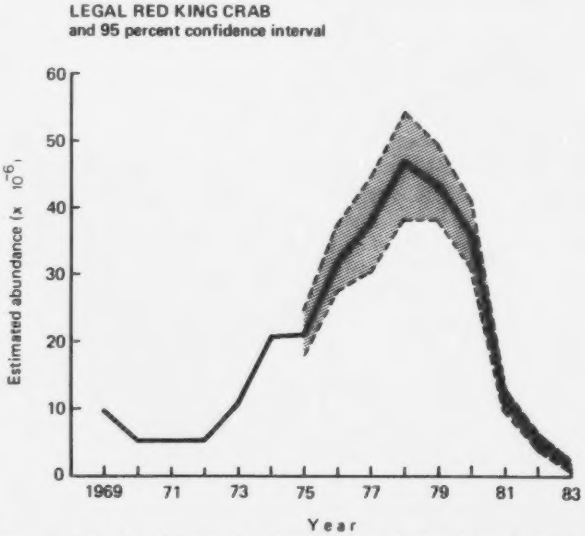

FIG. 1. Exploitable stocks of red king crab (male crabs with carapace length ≥ 135 mm) estimated from trawl surveys in the southeastern Bering Sea. Shaded region shows 95% confidence intervals.

Materials and Methods

Trawl surveys of red king crab grounds in the southeastern Bering Sea were first conducted by the U.S. National Marine Fisheries Service during 1955 (Weber and Miyahara 1962) and have been conducted annually since 1968. Methods were standardized in 1969 and computerized data sets date to 1970. Details of survey methodology are available in annual reports of the International North Pacific Fisheries Commission (e.g., Otto et al. 1984). Surveys were conducted primarily during June of each year and therefore assessed the stock at similar points in the annual cycle of molting, growth and reproduction.

The sampling program extends over most of the eastern Bering Sea shelf and utilizes a fixed grid of sampling areas, each 37 × 37 km (Fig. 2). At least one trawl-tow is taken centrally per sampling area, but additional samples (commonly at a geographical corner of an area) also may be taken. Carapace length (Wallace et al. 1949) and sex of crabs caught in the trawl are recorded. Area-swept estimates (Alverson and Pereyra 1969) are made for each tow to estimate density of crabs (number per unit area) and a stratified average density is used to provide population estimates for the stock within a specified habitat area (Otto 1986). Size frequencies can be plotted for the aggregated data from each year's survey and abundance estimates generated for crabs selected by specified criteria, such as size and sex. Data from 1971 were not used in this study because there was only partial coverage of the red king crab habitat during that year.

Size-frequency data for both sexes combined were plotted by 1 mm increments for each year's data in order to identify the smallest crabs regularly caught in surveys and to look for large size-frequency modes of juveniles. Both sexes grow at comparable rates until they reach sexual maturity, during or after their fifth year (Weber 1967). Using data for both sexes combined for crabs younger than 5 yr old provided larger sample sizes for analysis.

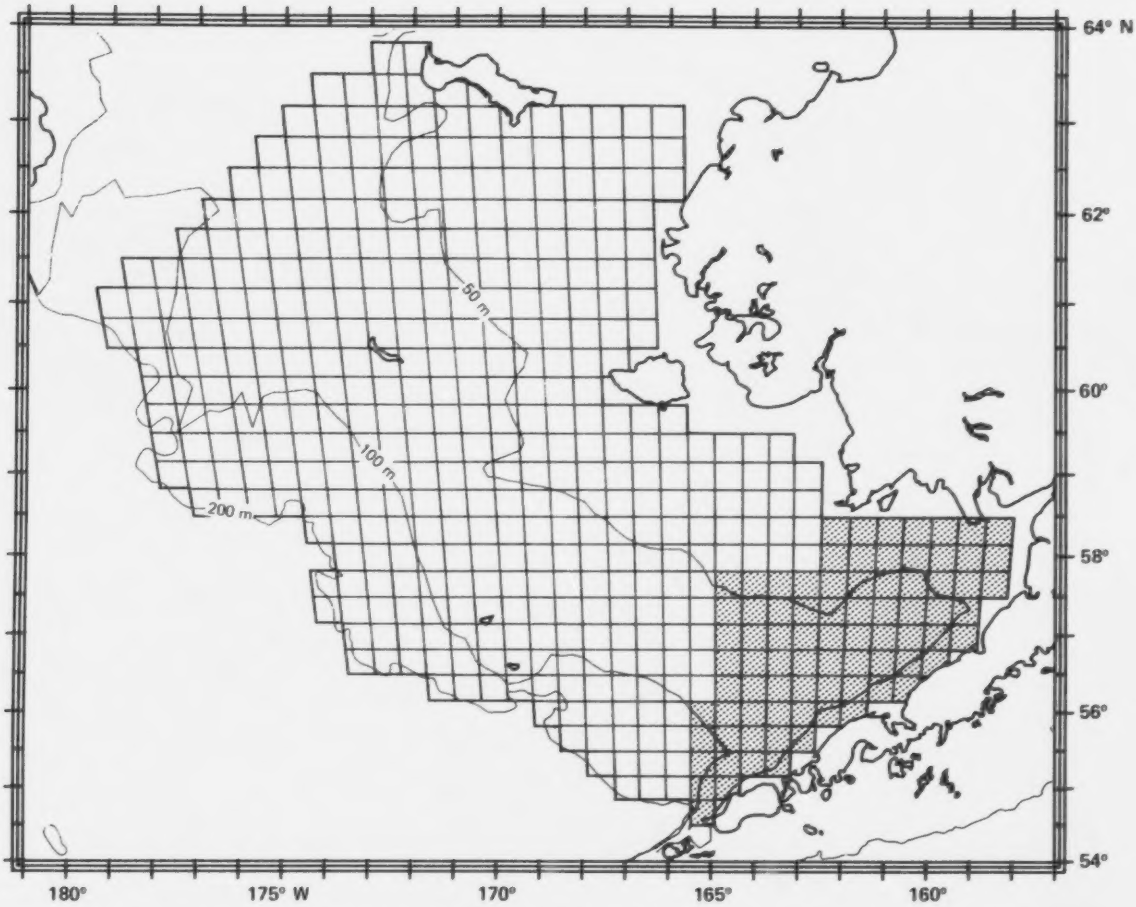

FIG. 2. Eastern Bering Sea shelf showing 50, 100, and 200 m isobaths; grid of sampling areas used during benthic trawl surveys; and red king crab grounds sampled annually since 1968 (shaded). Sampling areas in the grid are 37 × 37 km. Most of the shelf south of 59°N has been sampled annually since 1975.

Large modes in the size-frequency data for juveniles were delineated subjectively and the source(s) of crabs constituting these modes were identified according to (1) location(s) where they were sampled and (2) abundance of crabs in individual trawls. In addition, all data from 1970 to 1983 exclusive of 1971 were merged and average size-frequencies were plotted to examine the average relationship between sampled abundance and size. This was used to evaluate relative size-dependent differences in vulnerability of crabs to capture by the sampling gear.

Data from Weber (1967) and the growth models of McCaughran and Powell (1977) were used to estimate size ranges within which peak abundance of crabs of various ages would be expected (Table 1). This information was used to help identify ages of crabs represented in annual size-frequency data (Fig. 3). An age-class was considered to be adequately sampled if individuals occurred at a large number of stations with sample variances which were not excessive. Acceptability of data for juvenile age-classes was judged by comparison with survey data for adult crabs, for which there is considerable experience in surveying and stock prediction (Otto 1986). The continuity of size modes through successive surveys (years) was examined. A year-class was considered to be reliably indicated by the data if modes could be followed through at least 2 consecutive years.

The youngest age-class which could be sampled reliably (see Results) was selected, and an index of abundance was estimated for each year. The index was the estimated population of crabs within a narrow specified size range. This size range (from Table 1-D) was expected to catch only the peak of the mode of abundance, and not the entire year-class [cf. our values from Table 1 with probability distributions from table 7 of McCaughran and Powell (1977)]. A year-class was defined by the year during which larvae hatched. Hatching occurs during spring (Weber 1967; Haynes 1974). Relative recruitment success for each year-class then was calculated by dividing the index of abundance of the year-class by the estimated number of sexually mature female crabs present during the year of larval production. Females were considered mature if they were larger than the median size at which maturity is attained (90 mm CL).

TABLE 1. Length classes of red king crab up to age 6. Boundaries of size categories were derived by taking midpoints between mean lengths at various ages. Because of variable growth, each category contains only a portion of each age-class. Values are based on data given by (A) Weber (1967: table 12) and (B) McCaughran and Powell (1977: table 6). Averages of (A) and (B) were rounded to whole mm (C) and slight adjustments were made for convenience of calculations made in this study (D). All carapace lengths in the data base are reported in whole mm.

Model	Age (yr)	Carapace length (mm)	
		Male	Female
A. Weber (1967)	1	≤23.0	(same as males)
	2	23.1 - 47.5	(same as males)
	3	47.6 - 69.0	(same as males)
	4	69.1 - 86.0	69.1 - 84.0
	5	86.1 - 101.5	84.1 - 94.0
	≥6	≥101.6	≥94.1
B. McCaughran and Powell (1977)	1	≤23.0	(same as males)
	2	23.1 - 45.6	23.1 - 45.4
	3	45.7 - 68.4	45.5 - 67.4
	4	68.5 - 87.2	67.5 - 84.2
	5	87.3 - 104.6	84.3 - 97.3
	≥6	≥104.7	≥97.4
C. Averages of (A) and (B), rounded to whole mm	1	≤22	(same as males)
	2	23 - 46	(same as males)
	3	47 - 69	47 - 68
	4	70 - 86	69 - 84
	5	87 - 103	85 - 96
	6	≥104	≥97
D. Values used in present study	1	≤22	(same as males)
	2	23 - 46	(same as males)
	3	47 - 69	(same as males)
	4	70 - 85	(same as males)
	5	86 - 103	86 - 96
	6	≥104	≥97

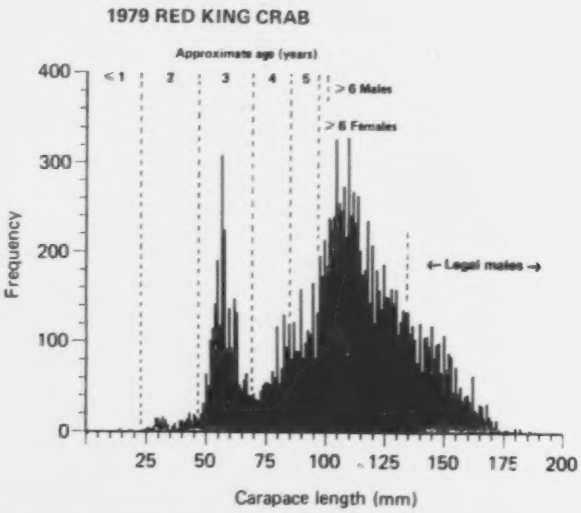

FIG. 3. Approximate age-size relationship for year-class modes from Table 1D shown with 1979 survey data. See text for interpretation.

Results

Size-frequency plots of crabs from each annual survey generally showed continuous distributions from 40 or 50 mm CL upward (e.g., Fig. 3-5). However, few individuals smaller than 50 mm were sampled and most of these came from only a few trawls each year. Well defined modes sometimes were present for crabs between 50 and 70 mm (1979 and 1981; Fig. 3,5), but these modes (apparently of 3-yr-old crabs) resulted from extremely abundant catches at a few, generally scattered, stations. More than 90% of individuals in this size range in each year came from only three tows taken in three non-contiguous grid areas. A discernable mode was present in 1974, and also was comprised mostly of individuals from only a few samples. These samples did not satisfy our criteria for defining a reliably sampled portion (size- or age-class) of the population. The large mode present in 1979 was not seen in subsequent surveys, while modes present in 1974 and 1981 each were clearly evident as modes of larger crabs during the following year (1975 and 1982, respectively).

Large size-frequency modes of juveniles also were present around 70 mm (1975), 72 mm (1982), and 85 mm (1976) (Fig. 4,5). During 1975 there also was a large number of crabs with carapace lengths in the range of 77–88 mm ($\bar{X}=82$ mm). These appeared to be less abundant than, but still distinct from, the mode around 70 mm and are defined as a secondary mode for this discussion.

Throughout all years represented in the data base, crabs meauring 70–85 mm and those in the modes noted above were caught in a large number of grid areas (from 35 to 41; Fig. 6) and, like larger crabs, showed generally gradual rather than abrupt geographical trends in abundance. Variances of estimated populations for the indexed juvenile crabs were somewhat larger than for adult females (mean coefficient of variation = 22% for 70–85 mm crabs, 11% for adult females), but were markedly reduced compared to smaller crabs. However, large size-frequency modes were not centered within the index size range of 70–85 mm. Rather, they were close to the upper or lower boundaries. Prominent modes of 1975 and 1982 were centered at or near the lower end of the preselected range (ca. 70 and 72 mm CL, respectively), while the less distinct secondary mode of 1975 (ca. 82 mm) and the prominent mode of 1976 (ca. 85 mm) were at or near the upper end.

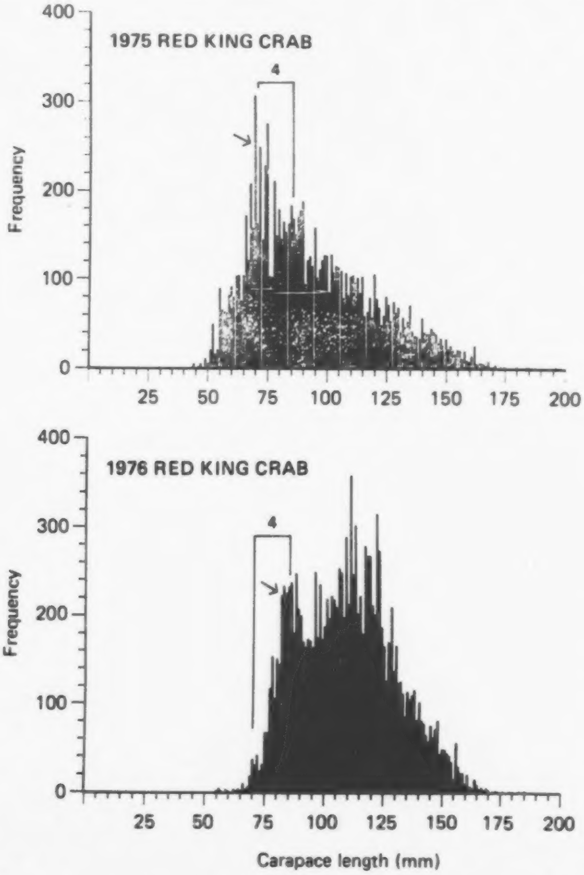

FIG. 4. Size-frequency distributions for 1975 and 1976 data showing prominent modes (arrows) which are not centered on the size range predicted for 4-yr-old crabs (shown by brackets). The large mode in each year probably results from a single year-class sampled in two successive years as 4- and 5-yr-old crabs, respectively. There may be a secondary mode in the region of 77–88 mm in the 1975 data.

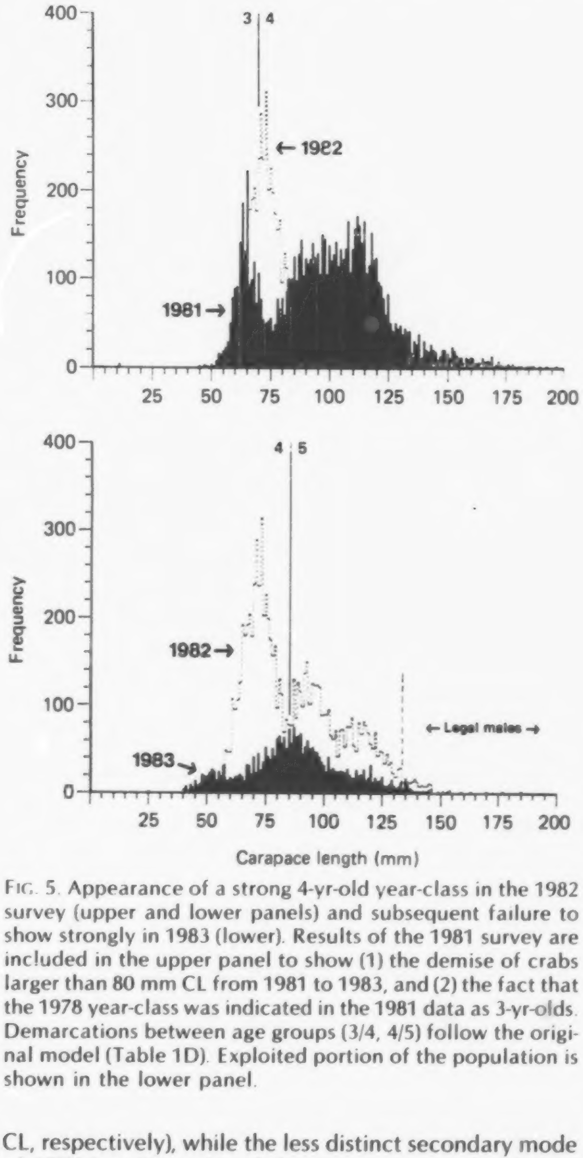

FIG. 5. Appearance of a strong 4-yr-old year-class in the 1982 survey (upper and lower panels) and subsequent failure to show strongly in 1983 (lower). Results of the 1981 survey are included in the upper panel to show (1) the demise of crabs larger than 80 mm CL from 1981 to 1983, and (2) the fact that the 1978 year-class was indicated in the 1981 data as 3-yr-olds. Demarcations between age groups (3/4, 4/5) follow the original model (Table 1D). Exploited portion of the population is shown in the lower panel.

Table 2 provides estimates of abundance for two size categories of crab: (1) 70–85 mm CL, established a priori for 4-yr-old crabs; and (2) 65–80 mm CL, based on size-frequency distributions about the prominent modes of 1975 and 1982. Both size criteria for 4-yr-old crabs indicate very strong year-classes originating in 1971 and 1978, but they yield somewhat different results quantitatively (Fig. 4A). The secondary mode of 1975 and the large mode seen in 1976 at the upper end of the 70–85 mm size range are discussed below.

Table 3 provides estimates of adult female populations (also shown in Fig. 7B) and a calculated index value relating female stocks to abundance of their progeny at age 4. Adult female crabs were at their lowest recorded levels from 1970 to 1972 (since the 1971 survey was incomplete, the estimate for that year was taken as the mean of the two neighboring years). The

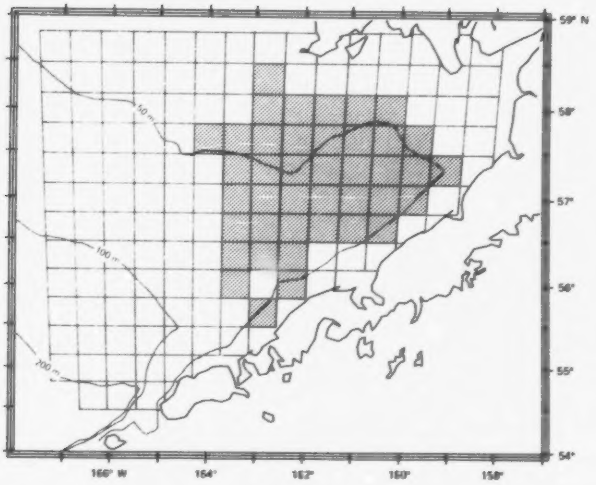

FIG. 6. Shading shows the 41 grid areas where juvenile red king crabs of 70–85 mm carapace length were caught during the 1981 survey; this was the smallest 4-yr-old year-class on record.

largest observed stock of adult female crabs occurred during 1977. The large year-classes of 1971 and 1978 were produced by two opposite extremes of adult female abundance.

The large juvenile population observed during the middle 1970's led to abundant stocks of adults during the late 1970's (Fig. 7B for females, Fig. 1 for males). In contrast, the large year-class identified during 1982 did not show up in 1983 (Fig. 5) or in subsequent years (1984 or 1985, unpubl. data).

Discussion

Trawl survey data examined in this study provide excellent coverage of the red king crab population of the southeastern Bering Sea. However, the surveys are conducted primarily for short-term forecasting and management of the commercial fishery (Otto 1986), and gear and methods consequently focus on sampling larger crabs. Early benthic stages are under-represented in survey data. In addition to selectivity of gear, patchy distribution of 2- and 3-yr-old crabs, probably due to podding behavior (Powell and Nickerson 1965), imposes problems in sampling. Patchiness was evident in the erratic catches of these two age-groups during surveys. Since large but infrequent catches of 2's and 3's were made at widely varying locations, it appears that tremendous sampling effort would be required for reasonable estimates of their abundance with the gear presently in use. Few age-1 crabs were caught, therefore little can be concluded about their broad-scale distribution or about appropriate sampling of this age-class for recruitment studies.

Crabs from 70 to 85 mm CL were sampled well enough that their numbers should permit satisfactory comparisons of abundance from year to year. Specifically, samples of this size class met our criteria of adequate number of crabs and reasonable sample variances relative to adult crabs, with which we have experience both sampling and forecasting. However, these numbers still provide only index values, whose accuracy may be affected in at least three ways.

First, selectivity of the gear is unmeasured. Average size-frequency distribution of crabs in the data base indicates that 4-yr-old crabs are caught in lower proportion to their abundance than older, larger crabs. The increasingly variable size of older crabs makes it impossible to quantify this relationship. Although the appropriate correction factor to apply in estimating the true abundance of 70–85 mm crabs is not known, the sampled estimate of abundance can be used as an index of year-class strength providing that catchability is not significantly biased by other conditions. One such source of bias might be abundance of larger crabs. We

TABLE 2. Estimated abundance of juvenile red king crab in two size groupings according to carapace length. Estimated population (*N*) and standard deviation (SD) are in millions of crabs for each sex and for both sexes combined (total). Coefficients of variation (*V*) are calculated for the total population estimates.

	Males				Females				Total					
	70–85 mm		65–80 mm		70–85 mm		65–80 mm		70–85 mm			65–80 mm		
Year	*N*	SD	*N*	SD	*N*	SD	*N*	SD	*N*	SD	*V*(%)	*N*	SD	*V*(%)
1969	7.7	3.0	9.4	4.6	5.2	2.1	8.9	4.9	12.9	3.7	28	18.3	6.8	37
1970	9.2	4.6	5.6	3.3	8.5	4.2	5.0	3.0	17.7	6.2	35	10.6	4.5	42
1971	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1972	3.1	1.8	1.4	1.2	3.8	2.0	1.8	1.4	7.0	2.6	37	3.2	1.8	56
1973	13.7	4.5	10.8	4.4	10.2	2.3	7.5	2.4	23.8	5.1	21	18.3	5.0	27
1974	19.3	4.4	15.8	4.0	18.7	4.3	15.8	4.0	38.0	6.2	16	31.6	5.6	18
1975	31.9	7.4	30.3	8.1	37.1	7.3	36.2	8.4	69.0	10.4	15	66.5	11.6	17
1976	19.9	7.4	9.6	3.9	21.9	6.8	10.6	4.3	41.8	10.0	24	20.2	5.8	29
1977	7.7	1.2	5.6	1.1	12.7	2.2	7.2	1.6	20.3	2.5	12	12.9	1.9	15
1978	12.3	4.7	5.8	2.2	11.3	4.0	6.3	2.5	23.6	6.2	26	12.1	3.4	28
1979	9.8	2.6	7.8	1.7	9.1	1.8	7.1	1.6	18.9	3.1	16	14.9	2.3	15
1980	13.2	5.3	8.8	3.8	16.0	6.0	11.4	5.0	29.3	3.0	27	20.2	6.3	31
1981	9.7	1.6	10.2	3.3	10.1	2.5	13.1	5.7	19.8	2.9	15	23.4	6.6	28
1982	42.3	12.1	54.3	14.6	46.0	13.3	49.8	14.0	88.3	18.0	20	104.1	20.2	19
1983	11.3	2.7	8.8	2.0	11.1	2.5	7.7	2.1	22.4	3.7	16	16.4	2.9	18

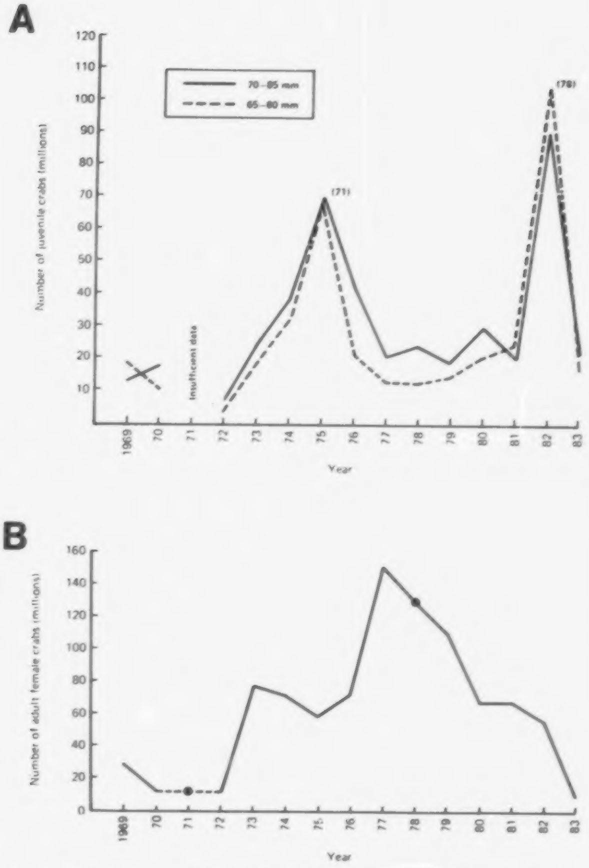

FIG. 7. Abundance of juvenile (A) and adult female (B) crabs estimated from trawl survey data, 1969–83. Relative interannual changes in abundance of 4-yr-olds (A) is indexed by sampled populations in two size groupings based on carapace length. Data from 1971 were insufficient for population estimates. The two prominent year-classes are labelled according to year of origin. Female stocks (B) producing the two prominent year-classes are denoted by dark disks; the abundance of females during 1971 was estimated as the average of 1970 and 1972.

note that in this time series very large numbers of 70–85 mm crabs were sampled during periods of both high and low stock abundance (Table 3).

Second, the size-range selected a priori for indexing the abundance of 4-yr-old crabs encompasses only a portion of the crabs from a single year-class even if the mean is centered within the range. Individuals from neighboring year-classes may be included as well. This is well illustrated in the data of Weber (1967) and the simulation of McCaughran and Powell (1977: table 7). This means that two consecutive moderate or strong year-classes would be difficult to separate in the size-frequency distributions and probably would produce inflated index values as a consequence of overlap in carapace lengths. Similarly, a strong year-class may overlap with neighboring year-classes to produce moderate index levels which would be difficult to interpret (e.g., data for the 1970 and 1972 year-classes sampled in 1974 and 1976; Fig. 7A). Inspection of the data is required to identify such problems and to take these into account when interpreting results. On the positive side, our data show that most weak and strong year-classes can be distinguished readily using appropriate index size ranges. The index provides a means for quantifying differences in year-class strength.

The third cause of potential bias is that the peak mode of abundance of a year-class may not occur symmetrically within the preselected index size range. This further affects the porportion of an age-class included in the calculated index value. This had some quantitative impact on our analyses (see Table 2) but did not qualitatively alter the results (Fig. 7). Visual inspection of size-frequency distributions and the apparent fit of the index size range to year-class modes is a recommended procedure. This can further resolve some difficulties, such as the prominent modes of 1975 and 1976 which occurred at the lower and upper ends, respectively, of our index size range. These modes were separated by 15 mm, a difference expected after one year's growth (Weber 1967). We thus interpret these modes as the same year-class sampled in 2 successive years. The mode sampled in 1976 (as 5-yr-olds) overlapped the index size range designated for 4's and probably inflated our index for the 1972 year-class (note the change in index values in Fig. 7A for 1976 using different size categories). Over all, however, there was no compelling reason to abandon the original index size range selected (70–85 mm CL), and this was maintained in subsequent analyses.

Modes at the lower end of the 70–85 mm size range in 1975 and 1982 are best interpreted as 4-yr-olds that

TABLE 3. Abundance of adult female crabs and index of success of progeny sampled at age four (= estimated abundance of juveniles in index size range ÷ abundance of adult females 4 yr earlier). The index size range of 70–85 mm (Table 2) was used in calculations. The adult female population for 1971 was estimated as the mean of 1970 and 1972. Indices of success for 1970 and 1972 year-classes may be inflated by presence of the strong 1971 year-class. The largest year-classes were from 1971 and 1978.

Year	Females[a] (millions)	Index of relative success of progeny
1969	28.50	0.836
1970	13.00	2.923
1971	12.60	5.476
1972	12.10	3.456
1973	76.80	0.265
1974	72.00	0.327
1975	58.90	0.321
1976	71.80	0.407
1977	150.10	0.132
1978	128.40	0.688
1979	110.90	0.202
1980	67.60	—
1981	67.30	—
1982	54.80	—
1983	9.70	—

[a] International North Pacific Fisheries Commission, Annual Reports give coefficients of variation (V) for females ranging from 6 to 20% ($\bar{X}$ = 11%) for the period 1975–1984; V was unreported in previous years.

were smaller than expected, rather than large 3-yr-olds. Both year-classes were sampled during the preceding years (1974 and 1981) as 3's which were in the appropriate size range and showed the expected patchy distributions. In contrast, the large modes in question (1975, 1982) came from widely distributed populations. This is consistent with the relative distributions of these two size groups throughout the data set, whether or not from large year-classes. Although data for 3-yr-old crabs are not adequate for a quantitative index of year-class strength, they add to the evidence of a large year-class when followed by a prominent mode of 4's in the following survey. Finally, the prominent mode of 1975 can be followed as a conspicuous mode in 1976 and as a marked increase in adults from 1977 to 1979 — proper timing for a 1971 year-class. The mode of 1982 could not be followed in subsequent years (see later discussion), but we have no reason to suspect that age-4 crabs were significantly different between the 2 years. We conclude that the major modes seen in this study are the 1971 and 1978 year-classes.

The smaller mode seen around 82 mm in 1975 is problematical; it is not large enough to be convincing of a strong year-class in the absence of additional information, yet it clearly appears larger than many of the year-classes indexed. The sizes of crabs included in the secondary mode appear too large and numerous to be primarily the same year-class marked by the mode at 70 mm, and it seems likely that many are from the previous year-class. However, the size of this (the 1970) year-class remains open to question. This situation arises partly from uncertainties inherent in surveys of marine populations when reasonable levels of effort are used (Collie and Sissenwine 1983). A contributing factor is the unknown contribution (in the size-frequency distribution) from the large 1971 year-class. We note, for instance, how the symmetry of neighboring year-class indices in Fig. 7 are affected by small differences in the size category selected for indexing. The size distribution of adult crabs during the late 1970's also does not solve the problem of identifying the strength of the 1970 year-class. The adult size-frequency distribution of the late 1970's could reflect dominance of a single large year-class from 1971 (cf. model of McCaughran and Powell 1977) and this would be the simplest interpretation. However, it is still possible that the 1970 year-class was large enough to contribute significantly. We can reasonably conclude that the 1970 year-class was substantially smaller than those of 1971 and 1978, but cannot say whether or not it was larger than the majority of other year-classes observed. Similar uncertainty attends quantitative evaluation of the 1972 year-class sampled at age 4.

Increases in female (Fig. 7B) and male (Fig. 1) adult crabs during the late 1970's which appear to be attributable largely to the 1971 year-class were preceded by moderate increases in stocks several years earlier. The patterns, beginning in 1973 with females and 1974 with males, suggest at least a moderate year-class originating around 1967. Unfortunately, the data do not permit a more detailed examination of this situation.

While the 1971 year-class went on to support record harvests during the late 1970's, the 1978 year-class did not appear at all strong during 1983 (at age 5, Fig. 5) or subsequently (1984 or 1985, unpubl. data). The apparent strength of the 1978 year-class and its mortality probably are not artifacts of sampling even though considerable sampling variability can be expected (Byrne et al. 1981; Collie and Sissenwine 1983; Otto 1986). Presence of the strong year-class was indicated in 1982 by positive samples in the same number of grid areas (36) and with similar sample variance as in 1975 (Table 2). The disappearance of this year-class paralleled a dramatic decline in the stock as a whole (Fig. 7B for adult females; Fig. 1 for adult males), and we therefore have no reason to regard the high 1982 index as erroneous. The decline in adult stocks has now persisted through 3 years, 1983–85, and leaves virtually no doubt about the demise of the population sampled during 1982. These findings indicate that large interannual variations in survival are possible both before and after age 4. The cause of the dramatic decline in recent years is unknown.

Interannual differences in year-class abundance observed by age 4 varied by almost one order of magnitude and were extremely significant in terms of the exploitable population. Since large year-classes occurred infrequently, patterns of year-class strength can be related unequivocally to large changes in commercial catches. Unfortunately, these data do not show when these differences were established during the first 4 yr of life. Indices of offspring success (index of abundance at age 4 divided by female stocks producing the year-class) indicate differences as large as 40 times. An outstanding survival rate to age 4 was noted only once during a 12-yr time series (1971, Table 3, taking note of the difficulty of interpreting the true strength of the two neighboring year-classes). This index could be improved in future by taking into account the size distribution and breeding season of females (primiparous *vs.* multiparous) and the effect that this has on fecundity. Abundance indices of 4-yr-old crabs showed no systematic relationship to stock size, since large and small year-classes were produced at times of both high and low levels of stock abundance. As with many other species, four important and interrelated questions remain unanswered: What factors were most influential in determining patterns of year-class size seen in this study; do the same principal factors tend to limit year-class recruitment in most years; do these same factors predominate regardless of the level of the stock; and are certain definable periods in life history most often involved in the recruitment-determining processes?

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Stock Assessment in Data-Limited Situations — The Experience in Tropical Fisheries and its Possible Relevance to Evaluation of Invertebrate Resources

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The lack of data suitable for application of conventional age-based stock assessment models, is a major limitation for both tropical fisheries, and many invertebrate fisheries worldwide. A brief review of some of the main characteristics of tropical fisheries is given, in the context of the problem of assessing invertebrate resources.

Techniques of parameter estimation developed recently for tropical fisheries, particularly for growth, mortality and overall production, may be readily adaptable to invertebrate fisheries. How these parameter estimation techniques are assembled into assessment methodologies and adapted to systems of fisheries management is not always clear from the literature. This paper recognizes eight different actual or potential methodologies that incorporate some of the above techniques, and gives short examples of their application in cases where these are not available in the literature. Methodologies suggested include those based on documented regularities observed between growth and mortality, dynamic and stationary size frequencies, resource mapping, estimators of fishing intensity and production per unit area, production modelling with mortality rates, and production modelling with biologically meaningful indices.

Le manque de données appropriées à l'utilisation de modèles classiques basés sur l'âge pour l'évaluation des stocks constitue une importante limitation pour les pêches tropicales et bon nombre de pêches des invertébrés, ceci au niveau mondial. L'auteur traite brièvement de certaines des principales caractéristiques des pêches tropicales dans le contexte du problème que pose l'évaluation des ressources en invertébrés.

Certaines techniques d'estimation de paramètres récemment élaborées pour les pêches tropicales, portant notamment sur la croissance, la mortalité et la production générale pourraient être directement adaptées aux pêches d'invertébrés. La façon dont ces techniques sont réunies en méthodes d'évaluation et adaptées aux systèmes de gestion des pêches n'est pas toujours clairement décrite dans les publications. L'aueur présente huit méthodes existant déjà ou pouvant être élaborées qui font appel à certaines des techniques ci-dessus et donne de courts exemples de leur application à des cas non traités dans les communications. Les méthodes présentées comprennent notamment celles basées sur la régularité observée et enregistrée ayant trait au rapport entre la croissance et la mortalité et les fréquences dynamiques et stationnaires des tailles, de même qu'à certains paramètres de la cartographie des ressources, des estimateurs de l'intensité de la pêche et de la production par surface unitaire et de la modélisation de la production par taux de mortalité ou indices biologiquement significatifs.

Introduction

Many of the problems faced by workers in tropical fisheries are shared by those working on invertebrate fisheries in all latitudes. These may include:

1) A general shortage of reliable commercial and survey data series.
2) Problems of determining ages of individual organisms, hence difficulties in applying conventional methodologies, e.g. cohort analysis by age.
3) Few staff trained in appropriate assessment methodologies and a shortage of funds, equipment and facilities.

Other problems more specifically faced by workers in the tropics in assessing both invertebrate and vertebrate resources are:

4) Short life spans of many important commercial species, and rapid growth rates.
5) High diversity of species and fishing gears, with consequent difficulties in effort calibration, especially for artisanal (inshore) fisheries.
6) Replacement of one or more dominant species in response to heavy fishing by formerly sub-dominant species. This may have occurred in some areas for cephalopods where partial replacement of formerly dominant fish species appears to have occurred under intensive fishing (Caddy 1983a).

Despite the above, there are other factors that may potentially act to the advantage of workers on stocks of tropical fish and invertebrates. For example, although diurnal/lunar/seasonal phenomena such as monsoons may all affect availability and catchability, the major seasonal temperature-related changes in catchability in, for example, trap fisheries of northern latitudes (e.g. Paloheimo 1963) are generally less pronounced in the tropics. Thus, analysing short-term intra-annual data may be less of a problem and Leslie–Delury methods have more ready application after allowing for natural mortality losses (e.g. Ishioka and Inoko 1981; Chien and Condrey 1985).

1) Given their short life spans, it follows that annual catches are closer to being in equilibrium with annual fishing effort than they are for long-lived species. For annual species the effects of changes in fishing pattern should therefore be perceived more rapidly.
2) For short-lived species, annual landings may even be a reasonable index of recruitment, if fishing effort is fairly stable.
3) Some types of habitats (e.g. coral reefs) are suspected of supporting a relatively constant production per unit area (see e.g. Marten and Polovina 1982), and it is easier, at least in the oceanographically unproductive, clear-water areas of coralline shelves, to map the extent of important habitats, especially since peak production outside upwelling areas in the tropics generally occurs within the 50 m isobath.

Present Approaches to Stock Assessment in the Tropics

The perception of, and potential and actual application of stock assessment methodologies developed in temperate waters to tropical fisheries, is now undergoing significant modification, as experience in the application of such conventional approaches has accumulated. It may be useful at this point to provide a brief overview of some of the main themes before going on to look at possible directions for future developments.

1) SUSTAINABLE YIELD APPROXIMATIONS

The most common approach adopted in the early stages of most tropical fisheries has been to use the yield approximation of Gulland (1971), namely $\mathrm{MSY} \hat{=} XMB_0$ where M = natural mortality rate, B_0 = virgin biomass and X is a scaling factor ($X \approx 0.4$ is now more often used than 0.5 as being a more conservative "conventional" value, in a procedure that has had its share of critics e.g. Francis 1974). The use of this "rule of thumb" with, for example, biomass estimates obtained from acoustic surveys, has tended to obscure the fact that we rarely have good values for M, but perhaps most importantly, it has on occasions led managers to believe that it is possible, and desirable, to move directly towards putative estimates of MSY obtained from earlier surveys: a strategy that can have serious long-term consequences (see e.g. Caddy 1983b). MSY is probably not in itself an appropriate criterion for managing most stocks (see later), and in the final resort the appropriate scale of fisheries development probably has to be determined empirically in each case in a series of steps, with feedback of analytical "control" variables from the fishery at each step to determine the response of the population at each level of fishing intensity.

2) FISHING INTENSITY AND PRODUCTION PER UNIT AREA

Fitting production models to simple catch and effort data has been a widely applied approach to a number of tropical fisheries over the last decade, but can lead to unfortunate results if attention is not paid to defining appropriate stock units or in calibrating effort, not to mention problems caused by a lack of knowledge of the biology of the resources and their response to fishing.

After more than a decade in which the original distinction made between fishing effort and fishing intensity (effort/unit area) has rarely been made in the literature on production modelling, the small unit size of many tropical stock units, as well as sedentary inshore invertebrates elsewhere, is leading to greater emphasis being given to the classic variable of fishing intensity and the associated measurements of the "productivity" (yield/unit area) of various environments. This leads to a realization of the practical importance of mapping resources and habitats as a precursor to formal "dynamic pool" approaches to stock assessment.

3) LENGTH FREQUENCY ANALYSIS

Using length frequency data as input to population analysis began early in the history of fish population studies, with development, for example, by Baranov (1918) of catch curves based on size frequency data, and the parallel development of the "Peterson" method of modal analysis by, e.g. Harding (1949) for separating different groups by age or sex in a sampled population. These techniques have found obvious applications for tropical fish and for invertebrates, where age reading is often difficult and costly.[1]

There have been numerous updates of these two basic approaches to size frequency analysis recently and it is probably still useful to distinguish them in the following brief overview, since they require rather different assumptions and criteria for sampling. It should be recognized, however, which is not always the case in the literature, that these techniques still need to be incorporated into a combined stock assessment methodology, as described later in the paper.

a) Analysing "Stationary" Size Frequencies

These are based on "pooled" samples collected over a year or more, and ideally should approximate equilibrium conditions under the action of steady recruitment and constant growth and mortality rates.

Included here are mortality estimates based on mean sizes (Beverton and Holt 1956; Ssentongo and Larkin 1973), longevity (Hoenig 1983), catch curves (e.g. Pauly 1983) and the approaches of Van Sickle (1977), Ebert (1973), Powell (1979) and Fournier and Breen (1983). This class of methods of estimating mortality and growth parameters from stationary size frequencies, also includes cohort analysis by sizes (best described in Jones 1984) and analyses of cumulative catch curves (Jones and Van Zalinge 1981). Various methods (Allen 1953; Jones 1984; Cadima 1983) for estimating the impact of changes in mesh size on yield from stationary size frequencies, also belong here.

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[1] Methodologies touched on here were the basis for a "Conference on the Theory and Application of Length-Based Methods for Stock Assessment", held at Mazara del Vallo, Sicily, 11–16 February 1985. The Conference Proceedings will soon be available from ICLARM (International Center for Living Aquatic Resources Management), P.O. Box 1501, Makati, Metro, Manila, Philippines.

b) Analysis of Sequential Size Frequency Samples

The dynamic nature of most tropical fish stocks means that assuming stationarity is likely to be misleading for samples taken at one time of year only. However, growth curves can be fitted based on sequential (e.g., weekly, fortnightly, monthly) samples, in which class intervals are small enough for separate modes to be picked out. If length frequency samples can be adjusted up to the total removals, mortality rates following recruitment may be estimated intra-seasonally from the log ratio of successive catch rates if q is constant, or by (single) cohort analysis. Two steps are obviously included here:

(i) Modal analysis of individual samples using manual/graphical methods, e.g. Cassie (1954), Bhattacharya (1967), or various computer-based routines, e.g. NORMSEP (Abramson (1971) and ELEFAN (Pauly and David 1981), Pauly and Caddy (1985).

(ii) Fitting growth curves to sequential intra-seasonal samples.

This is still a somewhat subjective procedure, remembering that when followed intra-annually, growth may be discontinuous throughout the year (e.g. Pauly and Gaschütz 1979). This incidentally can of course affect yield per recruit, depending on timing of effort application in relation to the growth stanza.

4) ACCUMULATION AND USE OF PARAMETER VALUES FROM COMPARABLE RESOURCES

In the long-term, a body of parameter values from taxonomically similar organisms in similar ecological niches is gradually building up in the literature. With caution, these values can be used to make order of magnitude estimates of population parameters. For example, Pauly (1978) documents published information on fish growth and mortality interrelationships, and Caddy and Csirke (1983) proposed a systematic approach to this goal in the case of parameters of the logistic model. A similar approach seems open in the case of invertebrate stocks, and especially for penaeid shrimps and rock lobsters in the tropics, the parameter values obtained from analysis of a new population should be scrutinized carefully in light of earlier estimates, so that fundamental errors in methodologies and assumptions can be avoided where possible.

Some Promising Methodologies for Invertebrate Stock Assessment

A distinction which is not always made in the fisheries literature is that between a technique (e.g. for estimation of a parameter), and an assessment methodology, which for analytical methodologies may involve several techniques for estimating parameters such as growth, mortality and age at first capture. For surplus production modelling, the method used for collection of catch and effort data, the subsequent calibration of variables such as fishing intensity, catch rate or overall mortality rate and the subsequent technique used for curve fitting, all comprise the methodology for assessment.

Although a clear-cut distinction into a fixed number of separate methodologies is not practical given that new combinations of elements arise in particular circumstances, the following eight actual and potential approaches to assessment seem worth distinguishing as being of potential interest for invertebrate assessment. Table 1 gives information on the necessary data sources, parameter values and techniques required for each methodology and literature reference to an example of their application. In absence of such published illustrations, a brief example is given in the text.

I. PAULY'S ASSESSMENT METHODOLOGY BASED ON FITTING VON BERTALANFFY'S GROWTH CURVE

One category of analytical procedures that can provide working estimates of population parameters with relatively limited (dynamic and stationary) length frequency data has come to be associated with Daniel Pauly (e.g. Pauly 1983), who has had a major impact in developing and adapting methodologies to tropical fish stock assessment. This approach, which ideally presupposes experience with, and estimates from, some or similar species in comparable areas, is solely based on length frequency analysis and on relationships derived between growth and mortality parameters. It can be briefly summarised as follows:

(i) The Von Bertalanffy equation for growth in length is fitted to sequential length frequency data, after using a modal analysis routine such as ELEFAN (Pauly and David 1981) or Bhattacharaya's method (Pauly and Caddy 1985), with or without compensation for seasonal growth stanzas (Pauly and Gaschutz 1979).

(ii) A working estimate of the natural mortality rate M is obtained from introducing growth parameters and the mean ambient temperature ($\bar{T}$), into a multiple regression equation already developed from a large set of known values of M regressed on known values of Von Bertalanffy parameters K, L_∞, and $\bar{T}$ obtained from the literature (Pauly 1978, 1983).

(iii) A recent value of total mortality rate, Z, is estimated from the slope of a "corrected" catch curve by size (Pauly 1983).

(iv) A recent value of fishing mortality is estimated from $\hat{F}=\hat{Z}-\hat{M}$.

(v) Size at first capture ℓ_c, is estimated from the left hand side of the "corrected" catch curve.

(vi) Resulting parameter estimates can be used in a variety of ways. For example, they could be entered in the Beverton and Holt (1966) yield tables to estimate the current position of the fishery on the yield isopleth, or used in a Thompson-Bell type of yield simulation (Ricker 1975).

TABLE 1. Main components and techniques involved in the stock assessment methodologies outlined here

Methodology	Variables/parameters used	Techniques used	Parameters estimated	Example
I. Pauly's methodology	a) Sequential size frequencies	Stratified commercial catch sampling for sizes + modal analysis	Von Bertalanffy parameters K, L_∞	Pauly (1983) and *Homarus americanus* (see text)
	b) Lengths, weights	Regression analysis	a and b of $w = a\ell^b$	
	c) K, L_∞, mean ambient temp., $\bar{T}$	Multiple regression M on $K, L_\infty, \bar{T}$	M	
	d) Stationary size frequency or mean size statistics	Log catch curve "corrected" for size at age Z as function of ℓ_c, L_∞, $\bar{\ell}$	Z, ℓc, $F = (Z - M)$ Z, $F = (Z - M)$	
	e) F, M (or M/K), ℓ_c, ℓ_t at age, length-weight parameters	Thompson and Bell Yield/Recruit or Beverton and Holt Yield Tables	(Change in) Y/R with ℓ_c, F, and/or M, (M/K)	
II. Jones cohort analysis with sizes	a) Stationary size frequency adjusted up to total removals	Stratified commercial catch sampling for sizes	—	See Jones (1984)
	b) " " "	Modal analysis.	Von Bertalanffy parameters K, L_∞	
	c) Annual effort and Z series	Paloheimo's method (or Ic above)	M (often a reasonable range of values used in absence of an estimate)	
	d) Guess F/Z (largest sizes), M/K, L_∞, (M)	Cohort analysis by sizes	$Z\Delta t$, F/Z, $F\Delta t$ by size group; No. survivors and yield for different F vectors	
III. Analytical assessment without growth rate	a) Series annual size frequencies or annual mean sizes and sizes at first capture (ℓ_c's)	Stratified commercial catch sampling for sizes mean sizes and ℓ_c, or catch curve analysis (sizes)	Annual values of $(Z/K)_t$	*Nephrops norvegicus* (see text)
	b) Estimate of average maximum size (L_{max})	$L_\infty \simeq L_{max}/0.95$	L_∞	
	c) Total annual effort exerted	Logbook or port interviews	$f_t, \bar{f}_t$	
	d) $\bar{f}_t$, $(Z/K)_t$	Linear regression	M/K	
	e) F, M (or M/K), ℓ_c, ℓ_t at age, length-weight parameters	Thompson and Bell Yield/Recruit or Beverton and Holt Yield Tables	(Change in) Y/R with ℓ_c, F, and/or M, (M/K)	
IV Resource mapping and comparing area-specific productions	a) Chart of fishing grounds, or remote sensing imagery by species habitats	Aerial or satellite imagery plus "ground truth", or observing fleet distribution Planimetry	Effective stock area and catch rate per unit area	Anon (1981)
	b) Mean catch rate per unit area by standard boat/gear in this and comparable areas	Compare catch rate with similar "fully exploited" grounds	Order of magnitude of expected catch at "full exploitation"	
V. Swept area estimates	a) Chart of fishing grounds, or remote sensing imagery by species habitats	Aerial or satellite imagery plus "ground truth", or observing fleet distribution Planimetry	Effective stock area and catch rate per unit area	[illegible] (1982)
	b) Estimate standard boat-hours fished annually with standard gear	Logbook or port interview	f_t	
	c) Estimate standard gear efficiency and effective area swept per unit effort	Field experiments on gear Calculate effective area swept per unit effort	q' F'	
	d) As per Ic) or IIc)	As per Ic) or IIc)	M	
	e) q', F', M, K, L_∞	Thompson and Bell yield per recruit simulation	Expected change in Y/R with effort for a range of M's	

VI. Production modelling with area-specific estimates	a) As for IVa) and b) for a series of ports/fishing areas where basic productivity/area is similar	As for IVa) and b)	Effective stock areas and catch rates per unit area for each port/fishing area	Multispecies near-shore production Dominican Republic (see text)
	b) Standard boat-day exerted per unit area annually in each area	Logbook or port interviews	Standard effort/unit area for each port/fishing area	
	c) Effort/area and yield/area for a series of areas	Regression fit to logistic or exponential models	f_{MSY}, MSY (per unit area, and for each individual fishing ground)	
VII. Production modelling with mortality rates	Time series of annual mortality rates Z_i, and yields or mean catch rates	Ia) and Id)	Z_i Y_i	Western Australian lobster (see text)
1. Fitting the mortality yield curve	a) Annual estimates of total yield from stock	Statistical sampling of commercial catch	$= {}_iZ_i$	
	b) Equilibrium approximation	See text	MSY, F_{MSY}, M	Gulf of Aden Cuttlefish (see text)
	c) Fit production model	Regression analysis	U_i	
2. Fitting catch rate on mortality rate	a) Estimate annual mean catch rate for standard boats	Log books/interview for sample fleet	Z_{MBP}, U_{MBP}	
	b) Regression of U_i on Z_i	Regression analysis	Z_{MSY}	
	c) Gian M or U_∞	Solve for other parameter (M or U_∞)		
VIII. Production modelling with biological measures of exploitation rate	Time series of:		Y_i	Kodiak king crab (see text)
	a) Total yield from stock	Stratified sampling commercial catch	"Exploitation index"	
	b) Some biological index which is believed to be related to exploitation rate	Biological sampling of commercial catch	"Maximum Yield Condition" defined	
	c) Fitting empirical relationship to a) and b)	Point of maximal production determined in terms of "Exploitation index"		

A degree of controversy surrounds this procedure, for example concerning the possible cumulative effects of errors and biases in fitting the growth curve on both the subsequent estimates of *M*, and hence on *F*, and thus subsequently on the best guess of the current position of the fishery on the yield per recruit isopleth. Despite this, the methodology has the merit of allowing yield computations to be initiated after only a relatively short initial investigation.[2]

II. COHORT ANALYSIS WITH SIZES

An approach to analysis of stationary size frequency data is the modification of Pope's cohort analysis by Jones described well in his 1984 review. Cohort analysis by sizes has of course been used for high latitude fisheries, but is included here for comparison, and because of its particular value for species that are dif- ficult to age. A disadvantage of this approach for many tropical resources, is that the error term increases with this method for *M* values much above 0.4.

The method requires input values for *M/K* and L_∞. An approximation that has been used for the second of these parameters if a growth curve is not available, is $L_\infty \simeq L_{max}/0.95$, where L_{max} is the largest fish reported from a well-sampled stock.

Given a guess of terminal *F/Z* for the largest sizes (which is not critical unless *F* is very low), this procedure allows computation of values for $Z\Delta t$, *F/Z*, and $F\Delta t$ at size, where Δt is the time to grow through a class interval at a given size. This procedure also furnishes some idea of gear selectivity. A simple extension of the method in fact allows effects of changes in selectivity and fishing effort to be estimated.

Even without a special *K* estimate, results from this procedure can be used as input to Beverton and Holt (1966) yield per recruit tables. However, if a growth curve has been fitted, the time interval Δt for growth through any given class interval is also available. This then allows estimates of *F* and *Z*, and if total catch is known, the number of individuals by sizes left in the sea can also be calculated.

The only "parameter" not readily available then is *M/K*. As noted by Beverton and Holt (1959), the ratio *M/K* tends to remain relatively more constant than *M* or *K* separately, so that published values for the mortality/growth ratio from taxonomically-related species should allow a reasonable range of values of *M/K* to be used. Some idea of the likely percent change in yield per recruit from a given change in size at capture and/or fishing mortality can then be found by modifying the F at size vector in the analysis. Here again, a relatively rapid initial analysis is possible, if pooled size frequencies of the catch over several years are available, assuming the fishery to have been relatively stable. A good example of this method is given in Jones (1984).

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[2] N.B. Although sets of data used in deriving the multiple regression mentioned above were for fish species, the method has given reasonably convincing results for crustaceans, e.g. penaeid shrimps (remembering that L_∞ should correspond to total length TL, not carapace length, CL). For offshore stocks of *Homarus americanus*, for example, if we take the mean of the five values for growth rate given by Thomas (1973) of $K=0.07$ (both sexes), and $L_\infty=258.2$ mm CL, converted to $L_\infty \simeq 76$ cm total length (TL) from $TL=(CL+0.13)/0.44)$ (Wilder 1953), and also assume a mean ambient temperature of 8°C, we obtain a value of $M=0.156$: quite close to that of $M=0.15$ obtained by averaging the wildly variable values tabulated in Thomas (1973), obtained by a variety of direct methods. Clearly this result could be further refined, but is simply intended to show that the method may be broadly generalized, at least until estimates of *M* from more direct methods are available.

III. ANALYTICAL ASSESSMENTS WITHOUT GROWTH RATE DATA

Various methods proposed by Beverton and Holt (1956), Ssentongo and Larkin (1973) and Jones and Van Zalinge (1981), are all simple and useful methods for obtaining estimates of Z/K (the ratio of annual mortality to Von Bertalanffy growth rate) from stationary size frequencies. More recently, Hoenig (1983) has provided several other estimators of Z from size statistics. If the Von Bertalanffy K estimate is available independently, obviously estimates of Z can then be obtained. However, even if growth rate is not known, annual values of $(Z/K)_t$ are an index of total mortality rate could be used directly in the production model approach of Csirke and Caddy (1983), assuming corresponding annual yield values were available, K remains constant, and problems of departure from equilibrium are not critical. An intercept of M/K on the abscissa at zero yield would then presumably be obtained.

Alternatively, assuming that it is possible to obtain a train of annual values for fishing effort (f_t) and values for $(Z/K)_t$ from size composition analysis by any one of the above methods, it seems possible to arrive at an estimate of M/K by a simple modification of Paloheimo's (1961) method, in which all terms in the relationship $Z_t=M + q\bar{f}_t$ are divided by the von Bertalanffy growth rate K which, as for M, is assumed constant over the range of observations.

Thus,

$$(1) \quad (Z/K)_t = M/K + (q/K)\cdot\bar{f}_t$$

where by analogy to Paloheimo's method:

$$\bar{f}_t = (f_{t-1} + f_t)/2,$$

since as noted by Paloheimo (1961), this significantly reduces standard deviation in estimates of regression parameters, compared with using the corresponding value for annual effort, f_t.

Example: Application of the method to Icelandic stocks of *Nephrops norvegicus*.

Using annual size frequency data for *Nephrops norvegicus* for Icelandic area 146 for 1962–75, given in Eiriksson (1979), the value of $(Z/K)_t$ was estimated annually from size frequencies, using the Beverton and Holt (1956) formulation, and compared with annual effort data (obtained from $f_t=Y_t/CPUE_t$: Eiriksson's table 130). Assuming provisionally that $\ell_c=35$ mm carapace length, corresponding to the legal minimum landed size of 10 g tail weight, was effectively the knife-edge selection point, and accepting Eiriksson's (1979) estimate of $L_\infty=80$ cm, then from Beverton and Holt (1956), values of Z/K could be estimated most simply by using $(Z/K)_t=(L_\infty - \bar{\ell}_t)/(\bar{\ell}_t - \ell_c)$ on the annual summed length frequencies of commercial catches of males from 1962 to 1975 (Eiriksson's table 127).

The regression of $(Z/K)_t$ on $\bar{f}_t$ (line A-A n Fig. 1) provides estimates of $M/K=2.426$ and $q/K=0.138$ with a low $r^2=0.151$. If Eiriksson's preliminary estimate of $K=0.1$ is used, this corresponds to $\hat{M}=0.243$ and $\hat{q}=0.0138$. However, examining data points in Fig. 1 more carefully, it is clear that those corresponding to the three earlier years of high fishing intensity lie well below the trend line for the following 10 yr, which may be a result of the time for the total mortality rate calculated from mean sizes to come into equilibrium with heavy initial fishing, given a relatively large virgin biomass. Without exploring this hypothesis further, the linear regression line was nonetheless fitted again without the 1963–65 points: (line B–B). This provided estimates of $\hat{M}/K=0.620$, and $\hat{q}=0.289$, with $r^2=0.75$. Again, if $K=0.1$ then $\hat{M}=0.06$ and $\hat{q}=0.029$. Although no objective estimates of M were available to him, Eiriksson concluded that M values below 0.1 or much above 0.2 were unlikely. In considering the present estimates in light of this opinion, we should note that these are strictly dependent on the value of $K=0.1$ used, which seems rather low.

IV. RESOURCE MAPPING AND ESTIMATES OF YIELD PER UNIT AREA

a) Resource Mapping

Given a chart showing the extent of species-specific habitats and/or fishing grounds, and information on landings by area of capture, estimates may be derived of invertebrate production per area of key habitat. Comparison of these production figures by area may reveal regularities that can, with care, be generalized more widely. The first requirement here of mapping important habitats, may be easier to accomplish in some cases than a species survey. Given that most benthic invertebrates are habitat-specific for some or all their lives, this mapping will aid greatly in for example, a proper stratification prior to a resource survey. This sort of mapping can be accomplished by aerial survey or from satellite imagery in clear water areas, or in northern latitudes or turbid waters, by benthic sampling, or with fishermen's cooperation, from log book analysis or port interviews.

Various estimates have now been compiled (e.g. Marten and Polovina 1982) of fisheries yield from different tropical habitats, including lagoons, coral reefs, turtle grass beds, etc. A number of these estimates have proved broadly comparable from similar habitats, even though exploitation rates, which are unallowed for, have been variable. If fishing intensity was the same, the assumption of a constant production per unit area may well have been valid. Most estimates of this kind have been made for the multispecies harvest, but some (e.g. estimates of production per unit area of spiny lobster for Puerto Rico and the U.S. Virgin Islands, Anon. 1981) have been for single species.

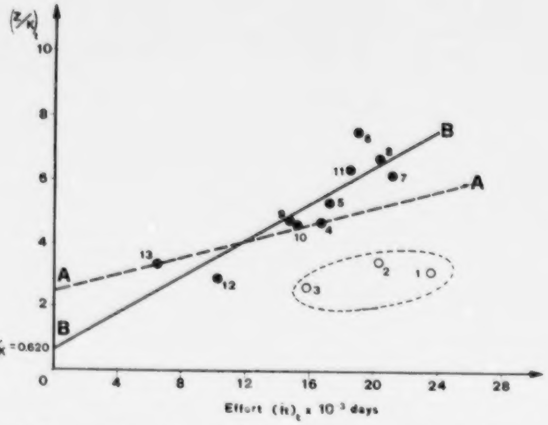


FIG. 1. Regressions of annual estimates of (Z/K_t) for Icelandic stocks of *Nephrops* in area 146 (Eirikkson 1979, see text) for 1963–75, on the mean effort $|\bar{f}_t = (f_{t-1} + f_t)/2|$ exerted in the same year (000'h). |Regression *A–A* including all points: *B–B* omitting the first 3 yr.|

V. SWEPT AREA METHODS

Again, given an estimate of the area of grounds and some idea of total effort exerted per area and per time interval, and an estimate of gear efficiency from say gear calibration trials, indices of total fishing mortality can be derived directly from fishing effort statistics. These could then be used under various assumptions in a simple Thompson–Bell yield per recruit calculation (Ricker 1975) to calculate effects of a closed season or effort change on yield (see for example, similar calculations in FAO/UNDP 1982 for Gulf shrimp stocks). An alternative with perhaps less chance of bias is to use a simple fishing mortality index for species i such as:

$$(2) \quad F_i' = \frac{1}{A} \cdot \sum_{j=1}^{n} C_{ij} a_j \cdot f_j$$

where f_j = total effort exerted by gear type j, and C_{ij} is the proportion of species i retained by gear of the stock in the area a_j swept per unit effort, within total stock area A_i. Values derived for F_i in different years could presumably then be used as input to conventional production models.

VI. PRODUCTION MODELLING USING AREAL ESTIMATES OF FISHING INTENSITY

Although the distinction between fishing effort and fishing intensity was stressed in the sixties, the general tendency recently has been to replace fishing intensity with fishing effort, assuming a constant (dynamic pool) relationship between fishing grounds and range of the stock, and perfect mixing condition. This assumption is a particularly weak one for sedentary, and mobile but territorial, species. This is especially true where early stages of the fishery are characterized by progressive geographical expansion of the fishing grounds, as those productive habitats closest to port are fished down to low densities, and new grounds further from port are discovered. Indeed, repeated sequences of fleet concentration and expansion may follow each year of good recruitment (e.g. Caddy 1975).

Some of the problems this phenomenon poses may be reduced for sedentary and territorial species by expressing yield per unit area of ground in terms of local fishing intensity, as suggested by Munro (1979). Given a series of fishing areas with similar basic productivity but subject to different fishing intensities, it is possible if the appropriate spatially discriminated catch and effort data are available, to fit a production model from only one or a few years of data. As noted by Caddy and Garcia (1983), individual production curves for any given area can then be derived from this combined "production-intensity" curve by multiplying both x and y variables by the area of individual grounds.

Again, this approach has to date been largely applied to multispecies resources, an example of which follows, but it has equal potential for single species assessments.

Statistics for the coastal fishery of the Dominican Republic are given in Gaugé and Arnemann (1982) in terms of annual landings, number of boats fishing, and area of the fishing grounds for each of the seven major ports in the Republic. Fitting the modified exponential model (Fox 1970) between the natural logarithm of mean annual catch per boat against number of boats per unit area allows the yield model

$$(3) \quad Y_i/A_i = (f_i/A_i) U_\infty e^{-b(f_i/A_i)}$$

to be drawn (line A–B in Fig. 2) where U_∞ is the virgin catch rate (assumed the same for all areas), and b is a regression parameter.

An estimate of the number of boats per unit area corresponding to the maximum yield per unit area (MYPA) of $\simeq 2\ \text{t}\cdot\text{km}^{-2}$ i.e. $f_{\max} = 0.8$ boats$\cdot$km^{-2}, is derived from yield curves A–B. Clearly, one data point, that for the port of "Samana" (Fig. 2), plays a major role in the regression fit, and when the jack-knife method is applied (see e.g. Efron and Gong 1983), in which individual points are dropped in succession with replacement, line A–C corresponds to a fit without Samana, and similarly, the shaded area encloses all other regression fits when one each of the other six points are dropped in turn. This suggests one rather cautious criterion to estimating yield parameters without making too many assumptions as to the underlying statistical structure of the data, namely, to give more weight to the more conservative of the seven estimates of $f_{\max}$ and MYPA. The most conservative yield curve (A–C) in Fig. 2 is that with the data point for Samana omitted. In the absence of more data points, this estimate (0.5 boats$\cdot$km^{-2} with MYPA$\simeq \doteqdot$ 1.75 t$\cdot$km^{-2}) may be less risky to adopt from a manager's point of view than that derived from a regression including all data points.

VII. PRODUCTION MODELLING WITH MORTALITY RATES

Csirke and Caddy (1983) put forward two approaches to fitting production models between annual yield or catch rate, and the total annual mortality rate (Z_t) as a substitute variable for fishing intensity (M assumed constant). These approaches have the advantage of

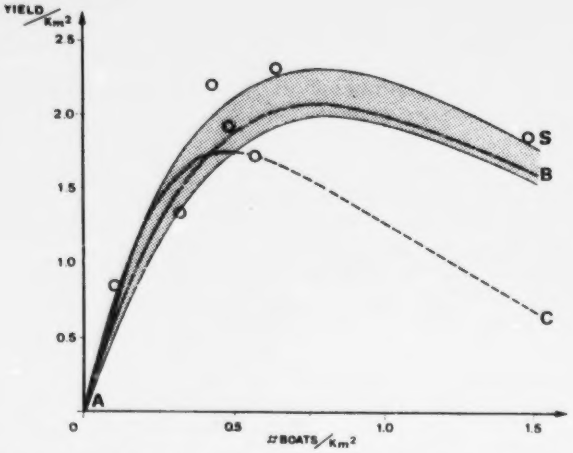


FIG. 2. Exponential production model (multispecies data) from fishing grounds adjacent to seven ports in the Dominican Republic (Gaugé and Arnemann 1982). Yield per unit area compared with fishing intensity for the same year on different but comparable areas. Line *A–B* is the fitted curve with all points: jack-knife estimates omitting 1 point fall within shaded areas (except for line *A–C* which is the line fitted with port Samana (S) omitted).

leading directly to analytic assessments allowing production modelling if size frequency rather than effort data are available, and avoiding difficult problems of effort calibration and fishing power changes that bias conventional effort-based production models.

Using properly designed and weighted size frequency samples, annual estimates of Z can be obtained by methods referred to earlier, and can be used in two main types of assessment. Csirke and Caddy (1983) suggested that if Z values came from catch curves or mean size statistics, they would be based on all age groups in the catch, and would be less liable to biases due to departures from equilibrium than the corresponding annual effort data. In the case of Z values derived from the log ratio of numbers in successive years, however, the following procedure may be an appropriate way of adjusting for gross departures from equilibrium if this is necessary (i.e. if the period to 50% mortality in the fishery, $t_{50} > 1$ yr).

EQUILIBRIUM APPROXIMATION WITH MORTALITY DATA

In the Gulland (1971) equilibrium approximation method, the current catch rate is compared not just with fishing effort in current year y, but with mean fishing effort during the k years up to and including year y, where k is the closest integer number of years to the time to 50% mortality (t_{50}) of an exploited year-class in the fishery at the mean level of effort prevailing during t_{50} (i.e., $k \leqslant t_{50}$). When using fishing effort data, the time to 50% survival of a given recruited year-class, or more relevant for our purpose, the time period from when there were twice as many individuals in the population as at the end of the current year y, is rarely known. The usual practice is to average effort over a constant number of years k, up to and including the current year, for the whole data series. Problems of applying such a constant period of averaging, especially in a rapidly developing fishery, are obvious, as is the impossibility, without mortality data, of choosing the appropriate averaging period for each year.

This problem appears less serious in the case of equilibrium approximation with annual mortality rates. Since for an exploited stock, $Z = (\bar{t} - t_c)^{-1}$, the reciprocal of the mean mortality rate over period t_{50}, up to the end of each year (y), is a direct estimate of time elapsed since the survivors at the end of the current year were twice as abundant: i.e., $t_{50} = \bar{t} - t_c = (Z_E)^{-1}$. One way of approximating to the equilibrium value for total mortality rate (${}_EZ_i$) is shown in Table 2, in which ${}_EZ_i$ for each year is approximated by a weighted mean of annual mortalities over a period t_{50} terminating at the end of each year of fishing.

Thus,

$$(4)\quad {}_EZ_i = \left[\sum_{i=y-k+1}^{y} Z_i T_i \right] \Big/ t_{50}$$

where T_i is the whole number or fraction of a year falling within the time interval t_{50} that terminates at the end of the current year. Thus, for year 9 in the hypothetical example in Table 1, $t_{50} = 2.273$ years, and

$${}_EZ_9 =$$

$$\left[Z_9(\times 1) + Z_8(\times 1) + Z_7(\times 0.273) \right] \Big/ 2.273 = 0.324$$

APPROACHES

The two main models suggested by Csirke and Caddy (1983) for fitting yield curves with mortality data have obvious applications to shellfish assessment. These are briefly described below with examples:

a) Fitting the Mortality-Yield Curve

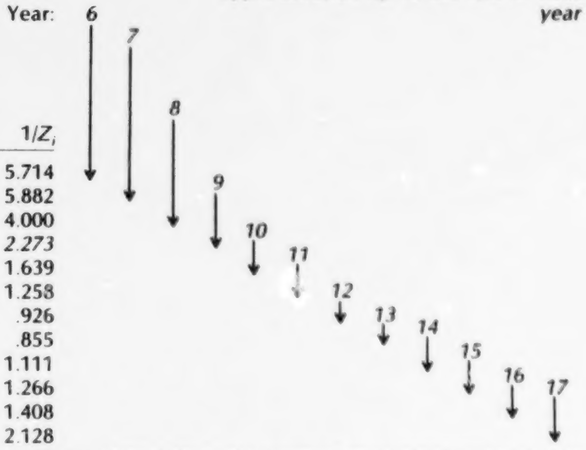
Substituting for annual fishing effort in Schaefer's version of the logistic equation by $(Z_t - M)/q$, with q and M constant, allows the logistic model (and potentially the exponential or other production models) to be expressed in terms of the equilibrium value of annual mortality rate, subsequently referred to for convenience as Z_t. Under logistic assumptions, this gives a parabola passing through the abscissa to the right of the origin where $Z_t = M$. Csirke and Caddy (1983) suggested two methods of fitting this parabola to yield and equilibrium Z values. The first of these, direct least-squares fitting of the second order polynomial $Y_t = c + bZ_t + aZ_t^2$, has so far usually been found to provide underestimates of M. The alternative approach advocated, fitting an abundance index, $U_t' = Y_t/(Z_t - M)$ against $(Z_t - M) = F_t$, in practice yields more reasonable values of M, even if it results in the undesirable regression characteristic of the same variable $F_t = Z_t - M$ occurring on both sides of the equation:

$$(5)\quad U_t = Y_t/(Z_t - M) = A - B(Z_t - M)$$

TABLE 2. One approach to equilibrium approximation using total mortality (annual) estimates when annual yield and mortality estimates are available. (Hypothetical data).

Year	Yield$_i$	Z_i	$1/Z_i$	$_EZ_i$
1				
2				
3				
4				
5				
6	7.5	0.175	5.714	–
7	12.5	0.170	5.882	–
8	19.0	0.250	4.000	–
9	35.0	*0.440*	*2.273*	0.324
10	40.5	0.610	1.639	0.544
11	39.5	0.795	1.258	0.757
12	30.5	1.080	.926	1.080
13	20.0	1.170	.855	1.170
14	26.0	0.900	1.111	0.927
15	29.5	0.790	1.266	0.813
16	27.5	0.710	1.408	0.733
17	29.0	0.470	2.128	0.602

Length of arrow gives appropriate duration for equilibrium approximation up to the end of each fishing year



This equation is fitted for different trial values of M, again either with functional or with predictive linear regression, in order to maximize r^2. The best fit provides an estimate of M and corresponds to fitting the equation:

$$(6)\quad Y_t/F_t = B_\infty - \left[\frac{B_\infty}{r}\right] F_t$$

where B_∞ = virgin stock size and r = specific rate of population increase.

From the regression fit we can estimate:

$$\hat{B}_\infty = A$$

$$\hat{r} = A/B$$

$$F_{MSY} = \hat{r}/2,\ Z_{MSY} = \hat{r}/2 + \hat{M}$$

$$\text{and MSY} = \frac{B_\infty F_{MSY}}{2}$$

Example: Fitting the equilibrium mortality-yield model to the western Australian rock lobster fishery.

A recent synopsis (Phillips et al. 1980) of biological data on the western (Australian) rock lobster *Panulirus cygnus* contains estimates of total mortality for two periods, one with a relatively low intensity of exploitation (1954/55 - 1960/61 seasons), and one of higher fishing intensity (1967/68 - 1972/73 seasons). Estimates of total mortality come from mean carapace lengths, using the equation:

$$(7)\quad Z_i = K(L_\infty - \bar{\ell}_i)/(\bar{\ell}_i - \ell_c)$$

for grade categories B-E which Morgan (1977) judged to be the best estimators of total mortality rate. Total landings for each of the above years come from table 27, and for the earlier period are read off figure 15 in the above publication. As such (and because data for the period 1961-66 are missing, when MSY conditions generally prevailed, according to the production model of yield on effort in the same publication), the data set and results leave a lot to be desired, but serve to illustrate the method of fitting the model.

Estimates of Z_i for 1954/55 to 1960/61 were adjusted for departure from equilibrium as described earlier (Table 1) to give values of the equilibrium mortality rate $_EZ_i$. Various trial values of M were tested to locate that giving the highest r^2 (Fig. 3). This was achieved with $M = 0.35$, and the resultant linear regression was:

$$Y_i/(_EZ_i - 0.35) = 43.477 - 41.464\ (_EZ_i - 0.35)$$

Multiplying this linear regression by various arbitrary values of $_EF_i = {}_EZ_i - 0.35$, allows the logistic production curve to be drawn (Fig. 4):

$$Y_E = 43.477\ (_EZ_i - 0.35) - 41.464\ (_EZ_i - 0.35)^2$$

This can be solved for MSY conditions, giving an estimate of:

$$F_{MSY} = a/2b = 0.524$$

This corresponds to estimates of $Z_{MSY} = 0.874$ and an exploitation ratio: $E_{MSY} = F_{MSY}/Z_{MSY} = 0.599$).

Estimate of MSY is then found from:

$$\text{MSY} = a^2/4b \simeq 11\ 400\ \text{t}$$

This is in excess of $7.3 - 8.6 \times 10^3$ t suggested from catch and effort data by Bowen and Chittleborough (1966), and Morgan (1977); reflecting the lack of data points for 1966 and 1967 when MSY conditions generally prevailed, with yields never exceeding 10 000 t. The

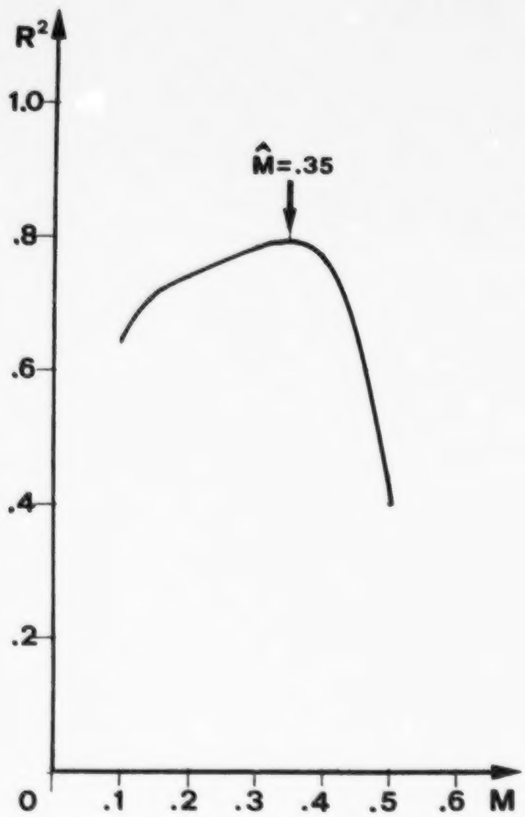


FIG. 3. Fitting the logistic model to mortality-yield data for the western Australian rock lobster data (Phillips et al. 1980). r^2 values from fits of "catch rate" on Z for different trial values of M (see text).

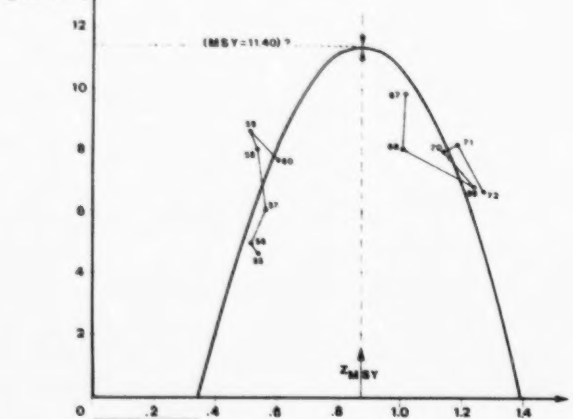


FIG. 4. Fitting the logistic model to mortality-yield data for the western Australian rock lobster data (Phillips et al. 1980). The yield curve for $M=0.35$.

value obtained for the natural mortality rate of $M=0.35$ may be more reasonable; lying between $M=0.23$ obtained by Morgan with Paloheimo's method, and a mean value of 0.58 (range 0.22–0.78) found by Bowen and Chittleborough (1966). We may surmise, however, that with a somewhat "flatter" yield parabola, passing through 7 000–8 000 t, the value of M might be rather lower than $M=0.35$.

b) Production Modelling with Catch Rate and Mortality Data

If annual catch rates (U_t) and mortality rates (Z_t) are available, but neither annual effort nor total landings, an estimate of the position of the fishery relative to the point of Maximum Biological Production (MBP) under the logistic assumption is possible (Caddy and Csirke 1983), where MBP results from the fishing mortality at which total production (natural deaths plus fishing) is maximized, assuming that production is approximated to by a parabola.

The relationship:

$$(8) \quad U_t = (U_\infty + b'M) - b'Z_E$$

of the form:

$$Y = A - BX$$

can be fitted as a functional or predictive linear regression, where U_∞ is the virgin catch rate and b' the slope of the regression. Given an independent value for either U_∞ or M, we can solve for the other parameter, and hence also for F_{MSY} since even if we have no estimate of current landings, under logistic assumptions, F_{MSY} corresponds to $U_\infty/2$. We can then also suggest what will be the *relative* change in landings caused by a change in the equilibrium value of Z_E.

Should reliable independent estimates of M or U_∞ not be available, it is still possible to fit the above relationship. This is useful in that the point on the abscissa corresponding to $Z_{MBP} = a/2b = (U_\infty + b'M)/2b'$ under the logistic assumption (i.e., MBP; Caddy and Csirke 1983), corresponds to conditions when total production for the system (fishing plus natural deaths) is maximized. Since this point is always to the left of MSY, it is in itself a useful benchmark, as is $F_{0.1}$ (Gulland and Boerema 1973). However, MBP diverges progressively from MSY as M increases.

Example: Preliminary production model assessment for cuttlefish, *Sepia pharaonis* in the Gulf of Aden

The intensive fishery for cuttlefish from 1967 to 1980 by Japanese trawlers in waters of the People's Democratic Republic of Yemen took place from May–June to September–November (Sanders 1979). The fishery was on a single cohort and this allowed estimation of mortality rates (very high) over the period of availability from:

$$Z = \frac{\log_e[c/f]_1 - \log_e[c/f]_2}{t_2 - t_1}$$

where $t_2 - t_1$ corresponded to mid-May–mid-October in most years (sexes combined). Geometric mean seasonal catch rates were calculated each year between the start and end of the periods of decline in catch rates chosen by Sanders (1979), and regressed on the seasonally adjusted total mortality coefficient Z_t, using both GM and predictive regression (Fig. 5). Considering the two variables as independent, the GM regression equation

$$\bar{U}_t = 349.30 - 71.81\, Z_t$$

was used to fit the upper parabola in Fig. 6.

$$Z_t\bar{U}_t = P'_t = 349.30Z_t - 71.81Z^2_t$$

(noting that since production $P = Z\bar{B}$, then $P' = Z\bar{U} = P/q$, and is an index of total production if q is constant).

MBP corresponds to $Z_{MBP} = 2.43$. This was exceeded in the early seventies, since which time mean catch rates have dropped significantly.

If the value of $M = 0.51$ obtained by Sanders (1979) is adopted, the second curve in Fig. 6 is obtained from:

$$\bar{U}_t = a - b'(M + F_t)$$

and provides an index of yield Y''_t defined by

$$Y''_t = F\bar{U}_t = Y/q = aF_t - b'MF_t - b'F_t$$

which can be used to calculate the proportional change in yield for a given change in fishing mortality rate. The lower parabola in Fig. 6 thus shows that if $M = 0.51$, MSY conditions should be prevailing around $Z_{MSY} \simeq 2.75$. Given that this method makes several broad assumptions, especially as to the shape of the mortality-production relationship, it may nevertheless be useful for obtaining a simple benchmark of exploitation in data-poor situations.

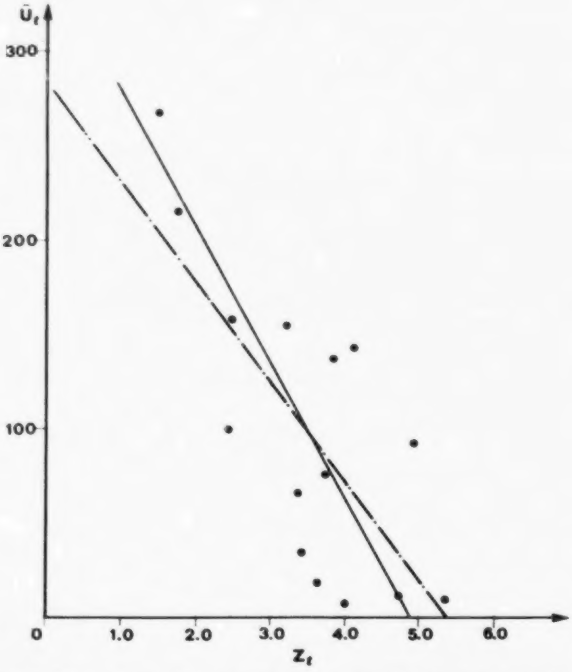


FIG. 5. Fitting a production curve to annual data on catch rate and mortality for the *Sepia pharaonis* fishery in the Gulf of Aden (Sanders 1979). Predictive (dash/dot line) and G.M. (continuous line) regressions of catch rate on mortality are shown.

VIII. PRODUCTION MODELLING WITH BIOLOGICALLY MEANINGFUL INDICES OF THE RATE OF EXPLOITATION

As one of the most useful tools available for fisheries management, the production model may be most simply regarded as an empirically determined control curve, describing past responses of the resource to changes in fishing effort. This is well exemplified by the GENPROD approach of Pella and Tomlinson (1969), where the shape of the production curve is dictated solely by "best fit" criteria to a flexible mathematical function without reference to any analytical explanation. In practice, there are often practical problems with this approach, especially in finding the "best" shape of curve by computer iteration to fit inadequate data. However, an assymetric production curve (e.g. Fox 1970) seems inherently likely where the plot of catch rate on effort decreases exponentially. This may represent, for example, a progressive bias in the effort measure with learning or density, and/or an inherent assymetry of response of the stock to fishing mortality. It seems worthwhile speculating whether there are other variables which might be easily measurable and biologically meaningful, and which, like fishing effort, are indirect measures of rate of exploitation. If so, these could form a variable configuration production curve when plotted against yield, using a routine such as GENPROD for fitting.

This concept, which is frankly speculative at present, suggests that a number of indices other than fishing effort, could be measures of the degree of exploitation. These might include one or more of the following:

(a) For crustaceans, an index of the percentage of soft-shelled (recently moulted or exuviate) individuals in the catch may be an index of exploitation intensity. Since moulting rate generally decreases with age, an increase in proportion of soft-shelled animals on an annual or indexed seasonal basis might imply a decreasing mean age of survivors.

(b) The percentage of immature recruits in the catch may be an indirect index of the degree of exploitation.

(c) For species with different catchability by sex, the sex ratio may itself be an index of exploitation rate.

Care obviously has to be used in interpreting plots of yield against any of the above variables, in that good recruitment years may affect these indices just as they can affect those measures of Z based on mean size alone. Extrinsic information (e.g. an independent estimate of recruitment) is highly desirable as an aid to interpretation.

Example: **Percentage exuviates and yield stock 3 for the Kodiak king crab fishery (Jackson and Manthey 1969).**

Speculation that the percent exuviates might be an index of the degree of exploitation is supported by

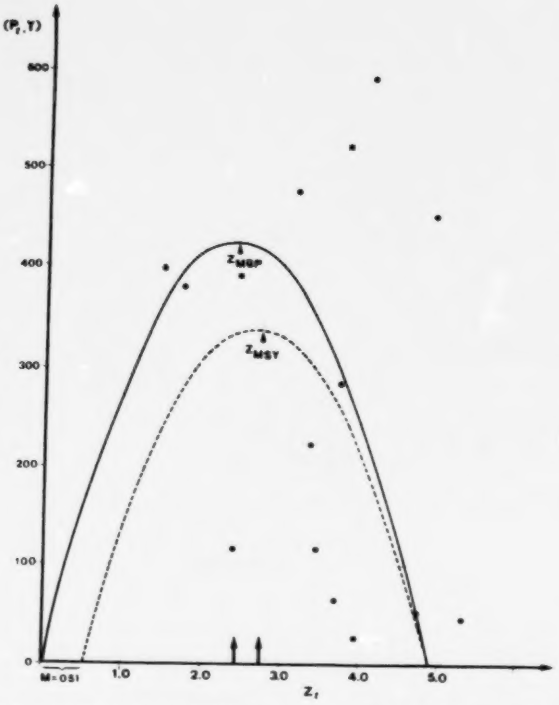


FIG. 6. Fitting a production curve to annual data on catch rate and mortality for the *Sepia pharaonis* fishery in the Gulf of Aden (Sanders 1979). Annual estimates for production index P' for 1967-68 and from 1970-80 are plotted against total mortality coefficient (upper solid line is production curve derived from S). The lower curve is the yield index for $M = 0.51$ (see text for definitions of P', Y').

Powell (1967), who shows that moult frequency drops with age for king crab as for many other crustaceans, so that moulting of large crabs only occurs every few years. Plotting yield against percentage of exuviates for stocks off Kodiak Island (Jackson and Manthey 1969) suggested that a skewed production curve could be fitted to data for 1960 to 1968 and this was done for a variety of values of an arbitrary scaling factor m in an equation of the form:

$$(9) \quad Y_i = X_i \left[\alpha - BX_i\right]^{1/m}$$

This was fitted by successive approximations and gave a reasonable ($r^2 = 0.87$) fit for scaling factor $m = 2$ (Fig. 7). The tentative yield equation in Fig. 7 is described by:

$$Y_i \text{ (millions of lb)} = \text{PEX}_i \left[0.2935 - 0.0034 \text{ PEX}_i\right]^{1/2}$$

with an apparent maximum yield at 8 074 t (17.8 million lbs) corresponding roughly to 55% exuviates in the catch. Two obvious criticisms can be made of this model as a preliminary attempt at assessing this stock:

(a) The 1960-61 point is the only one on the left-hand side of the curve. If it were absent however, a linear relationship with negative slope would still show that yield fell off with increase in exuviates over the time period considered; and

(b) some ascending relationship on the left-hand side, such as that shown, must be the case since lightly fished stocks of crabs are generally dominated by large, old individuals. However, the curve would not go through the origin as shown, but through the queried point to the right of the origin in Fig. 7, which corresponds to the percentage exuviates in the virgin stock. At the very least however, this fit would suggest caution be exercised by managers when the percentage of newly moulted or soft-shelled individuals in the stocks rises above 50%.

Discussion

1. THE SOCIO-ECONOMIC CONTEXT FOR STOCK ASSESSMENT IN DEVELOPING COUNTRIES

The context for stock assessment in many tropical areas often includes, as noted, a shortage of funds, personnel and equipment, and historical data. It is also relevant to note that although many national departments of fisheries since the late seventies have been training staff to take on the task of managing resources in their extended economic zones (EEZs), in many cases, conditions permitting implementation of scientific management measures do not always exist.

The immediate needs are for methods of assessment that are cheap and easy to apply, and allow an early start at analyses, preferably without a long time series of data. A similarly short time span for arriving at rapid, if approximate, assessments is required by investment banks and aid agencies. Here, the danger is extrapolat-

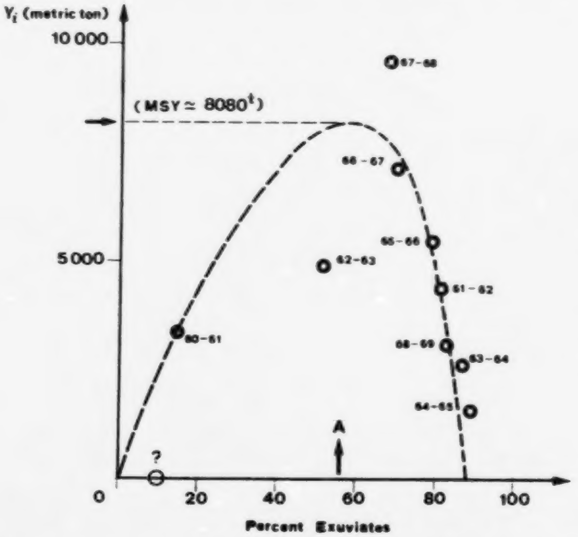


FIG. 7. Tentative fit of skewed production model for a local king crab fishery (Stock 3 off Kodiak Island from Jackson and Manthey 1969), in which the percent exuviates (PEX) in the annual commercial samples is considered an indirect measure of degree of exploitation in the stock (A = optimum PEX). The percent exuviates apparently corresponding to maximum yield is 55%. The queried circle poses the question: What is the (non-zero) percent exuviates for a virgin stock?

ing from conditions and methods used in high latitudes, which may result not only in inappropriate yield estimates and too large a scale of development leading to overexploitation and gear conflict, but also in placing long-term reliance on what are essentially short-term methods of assessment.

Although the need for "quick and easy" approaches to assessment exists in the short-term for both invertebrates and other resources, early rough parameter estimates need to be refined later in light of accumulated time series collected by a fisheries statistical service, hopefully set up early in development. Conventional types of data, especially catch rates, fishing effort and size composition need to be collected, not to mention more extensive use of commercial size category data. For invertebrates with their diversity of life histories, it is the author's conviction that measurement of biologically meaningful variables may yield better results than a poorly implemented sampling of catch and effort data alone.

2. EXTRINSIC VERSUS INTRINSIC MEASURES OF THE STATE OF THE STOCK

One of the main distinctions that should be made between those "biological" variables discussed here, such as mean size, percentage exuviates, sex ratio, etc., and the various measures of fishing effort conventionally used in production modelling, is that the former types of variables measures how the stock is *affected* by fishing and other influences. Measure of fishing effort, after massaging to remove learning factors and departures from equilibrium, constitute our best hypothesis as to the fishing mortality exerted. However, their *effect* on the stock can only be judged indirectly, e.g., from an apparent change in abundance. Both types of measures are biassed by environmental influences on the stock, which in the case of fishing effort acts through undetected changes in catchability, and in the case of size frequencies, acts through undocumented changes in growth and recruitment. In both cases, excessive dependence on only one source of information on the state of the resource seems unwise.

The conclusion that could be drawn from the above distinction is that the onset of "critical conditions" in the stock, such as recruitment failure, recruitment overfishing, etc., might with experience be eventually detectable from intrinsic biological indices in a way that is not possible with extrinsic indices such as fishing effort alone.

The other advantage that seems to be offered by biological indices that is particularly relevant to developing countries, is their cost effectiveness. Useful indices of the state of the stock (such as abundance in commercial size categories), may already be available from markets and processing plants. Other variables discussed here can be measured at points of landing at the same time as data are collected on the level of landings themselves, without the need for a separate log book system, or cross-calibration of data from different gear and vessel classes, for differences in fishing power. This is not to say that some measure of fishing effort is not desirable, as it certainly is for economic studies, but that in the case of a very diversified fishery this measure might be reduced to the maintenance of an up-to-date registry of fishing boats by gear type, size, etc., plus some information on the effective length of the fishing season.

As a final conclusion it should be noted that for most of the methods described here, there is no long history of application, and whenever possible results of these methods should be compared with methods of assessment now in use. Invertebrate fisheries in high latitudes appear to offer considerable potential for such a comparative approach, given their diversity, and given the existence in many cases of data series for biological variables that have not yet been used in stock assessment for lack of an appropriate methodology.

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A Disaggregate Model for Sedentary Stocks: the Case of South Australian Abalone

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SLUCZANOWSKI, P. R. 1986. A disaggregate model for sedentary stocks: the case of South Australian abalone, p. 393–401. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

The study focuses on solving problems associated with managing sedentary and widely distributed stocks caused by unrepresentative sampling, inadequate mixing of the stock and the complex nature of effort. A pulse fishing model is developed and applied simultaneously to a number of stock divisions of the South Australian abalone fishery. Variations of legal minimum length and periods of closures have varying effects on biomass yield per recruit and egg production per recruit, which lead to different risks to future recruitment. Modelling alternative management strategies highlights these compromises and shows that the fishery can be tuned closer to desired objectives with more complex controls which are more difficult to administer. A substantial decrease in egg production through the combined effects of increasing effort and the retention of current size limits is demonstrated and changes to legal minimum lengths are proposed to ensure the medium-term security of the stock for a small reduction in yield.

La présente étude vise à résoudre les problèmes associés à la gestion de stocks sédentaires cosmopolites, problèmes causés par un échantillonnage peu représentatif, un mélange inadéquat du stock et la nature complexe de l'effort. On a élaboré un modèle de pêche intermittente qui est appliqué simultanément à un certain nombre de divisions des stocks d'ormeau du sud de l'Australie. Des variations de la taille légale minimale et des périodes de fermeture ont diverses incidences sur le rendement de la biomasse par recrue et la production d'œufs par recrue, incidences qui portent différents risques pour le recrutement futur. La modélisation d'autres stratégies de gestion fait ressortir ces compromis et montre que la pêche peut être mieux synchronisée avec les objectifs visés à l'aide de contrôles plus complexes quoique plus difficiles à administrer. On démontre que les effets combinés d'un effort accru et le maintien des limites actuelles de la taille entraîneront une baisse importante de la production d'œufs. Des modifications des longueurs légales minimales sont proposées afin d'assurer la sécurité à moyen terme du stock même si le rendement doit légèrement baisser.

Introduction

The South Australian abalone fishery is based on two species: the greenlip abalone, *Haliotis laevigata* Donovan, and the blacklip abalone, *H. rubra* Leach. Commercially exploitable stocks are found over about 2000 km of coastline (Fig. 1), usually in dense aggregations and often on isolated reefs. The species are sedentary and slow growing. Because the larvae have a pelagic lifetime of only a few days, recruitment in any substock is largely independent of the state of others. Consequently recovery would be slow should a catastrophe occur to a substock.

Commercial exploitation of abalone in South Australia began in the mid-1960's, with production rising to 998 t meat weight in 1982/83. Fishing effort is restricted through limiting the number of divers to 35, each licensed to operate in one of three zones. Since transfers of licences were first permitted in 1981, most have changed hands. New entrants who bought into the fishery are generally young and highly motivated, resulting in a significant recent increase in diving hours. Catch rates have remained relatively stable at about 22 kg/h diving time.

Divers use hookah breathing gear and operate from trailable boats. Each area containing abalone is typically fished intensively over a short period until almost all abalone over the legal minimum length have been taken. The area is then left to recover. The pattern of exploitation is influenced by distance from home, weather conditions, expected catch rates at various sites, and the activities of other divers.

Until early 1984, a uniform legal length of 130 mm was applied to protect part of the spawning stock. The restriction applied to both species and all zones, principally because of the ease of administration and enforcement. However industry members have recently expressed concern at the possibility of recruitment overfishing as a result of increased fishing effort. This has been substantiated by their reported observations that some greenlip abalone stocks in areas W2 and W3 of zone W (Fig. 1) appear never to have recovered from intense fishing pressure. Management of the fishery is now under review and several improvements to management of the stock have been suggested to take account of the differing population dynamics characteristics of sections of the stock. These include differential size limits and closure policies, or rolling closures which provide a means of maintaining economic production while closing areas for substantial periods.

The main aim of managers of the fishery is to preserve and maintain the stock, while also ensuring the economic viability of the fishery. Because abalone are sedentary and widely distributed over a number of identifiable reef areas, the biological and population characteristics of a simple sample are not representative of the whole stock as required by most traditional fisheries models. Furthermore, the complexity of the fishing operation is such that fishing effort is hard to define so that catch rates are of limited value in estimating abundance.

The purpose of this study is to overcome such difficulties by determining how various combinations of controls on legal minimum length l_R and closure strategy can be used to achieve management objectives. These controls may be either aggregate, in that a single rule is applied to the whole fishery, or disaggregate, where a different combination of controls can be tailored to meet the particular requirements of each area. Effects of various management options on long-term biomass yield per recruit and egg production per recruit are investigated, taking account also of their utility, risk and ease of administration.

Sedentary disaggregate stocks present special problems which make them intractible to analysis by most conventional fisheries models for two reasons: the non-representative nature of sampling and the complex nature of fishing effort. To be useful for analysing widely distributed sedentary stocks, a model must be capable of being applied easily to a number of substocks at the same time, allowing for different levels of knowledge and different states of each.

In addition to suggesting management schemes, a method of assessing the consequences of management methods currently in operation also would be useful. Age-structured models are impractical in such situations because monitoring age structures in each of a large number of independent abalone substocks appears to be beyond the finances of most management agencies. Surplus production models rely on the axiom that catch per unit effort is proportional to the population biomass. This assumption is unlikely to be justified because catch rates are determined mainly by physical limitations associated with handling the catch, and therefore remain constant, providing no abundance information until low densities are encountered (Beinssen 1979). Furthermore, a decline in population biomass caused by reduction in the number of reefs may not be reflected by changes in overall catch rates, which may be determined by other stable reefs. Similarly, the Beverton–Holt model has the disadvantage that it requires a measure of fishing mortality and a function relating it to fishing effort. For the same reasons, both of these may be impossible to obtain.

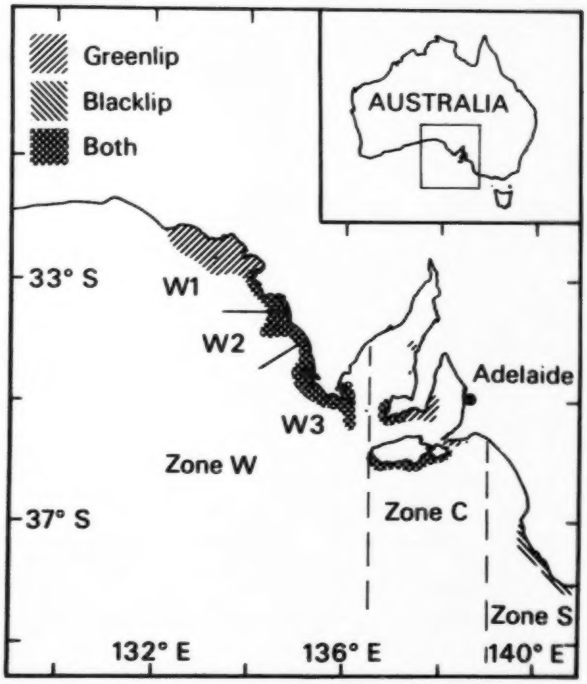

FIG. 1. Distribution of commercial stocks of greenlip (*Haliotis laevigata*) and blacklip (*H. rubra*) abalone in South Australia showing the three zones (W,C,S) and the three areas in zone W (W1,W2,W3).

Sluczanowski (1984) developed a model for a fishery in which a substock is subject to periodic (pulse) fishing of high intensity down to the legal minimum length l_R. In such cases, the period P between successive fishing visits to each substock often can be used to measure the rate of exploitation over the medium term. The model shows how both long-term biomass yield and egg production per recruit to the fishery depend on each combination of l_R and P. This model is useful to managers because, unlike fishing mortality F, P is an index of exploitation rate over the medium term which is familiar to those associated with the industry on the basis of experience and inspection and can be extracted from available catch and effort statistics. It can also be controlled by the use of effective closures.

Isibasi and Kojima (1979) used a similar model for analyzing yield per recruit and a number of models have been developed which assess the effects of management controls on variables directly linked to recruitment such as "average unexploited spawning stock biomass" (Beddington and Cooke 1983) or "eggs per recruit" (Campbell and Robinson 1983).

Methods: Model and Data

Sluczanowski's (1984) model, which is similar to that of Beverton–Holt (1957), describes how the biomass yield per recruit and number of eggs produced per recruit depend on the legal minimum length l_R and the period P between intensive fishing visits to the substock.

The model assumes that all individuals above legal size are removed at each visit of fishermen to the stock. Reports from divers and direct observation confirm that this happens in practice, especially for greenlip stocks in zone W, which are mainly collected from the exposed surfaces of reefs and small boulders surrounded by expanses of sandy bottom. The model also assumes that recruitment to the fishery is continuous throughout the year, because spawning is known to occur over about five months (Shepherd and Laws 1974) and growth between individuals varies significantly before they enter the fishery at about 4 yr age (Shepherd and Hearn 1983). These features ensure that there is a continual supply of abalone at the legal size limit. Individuals are assumed to release eggs continuously throughout the year, at a rate proportional to the number of eggs produced in a year by an individual of a given weight at the start of the spawning season. The assumption was justified in the knowledge that differential growth of individuals and the sporadic pattern of visits by fishermen to particular reefs average out any such seasonal effects. Adding a factor to account for seasonality would overly complicate the model. Two other assumptions were that the two species do not interact biologically and that the dynamics of the system are deterministic.

In the model, the relative number of fish in an age-class of age t, $N(t)$, is given by the equation:

$$N(t) = \exp(-Mt) \text{ for } 0 \leqslant t \leqslant t_\lambda$$

where M is the instantaneous rate of natural mortality per annum and t_λ is the maximum attainable age. The increase in length $l(t)$ of individual abalone is modeled by the von Bertalanffy growth curve with parameters L_∞ and K, while the weight $w(t)$ is related to $l(t)$ by parameters a and b:

$$l(t) = L_\infty\{1 - \exp(-Kt)\}$$
$$w(t) = a\,\{l(t)\}^b$$

The biomass of an age-class $B(t)$ reaches its maximum B_m at age t_m:

$$B(t) = N(t)w(t)$$
$$B_m = \max B(t) = B(t_m)$$

$\bar{B}(t_R,P)$ is the proportion of the maximum biomass yield per recruit B_m that is harvested on a long-term basis by successive fishing visits separated by period P with age at first capture t_R, corresponding to the legal minimum length l_R.

$$(1)\quad \bar{B}(t_R,P) = \left\{\int_{t_R}^{\min(t_\lambda,t_R+P)} B_t dt\right\}/PB_m$$

The instantaneous rate of egg release by an individual of weight $w(t)$ was assumed proportional to the number of eggs produced in a year by an individual of a given weight $w(t)$ at the start of the spawning season, $E(t)$, which is modelled by a positive piecewise linear function with parameters e_1, e_2 and t_F, the age at first fecundity:

$$E(t) = 0 \qquad \text{for } 0 \leqslant t \leqslant t_F$$
$$E(t) = e_1 w(t) - e_2 \quad \text{for } t_F < t \leqslant t_\lambda$$

The number of eggs per recruit shed by an age-class during its lifetime up to age t, $A(t)$, reaches a maximum A_m at age t_λ:

$$A(t) = \int_{t_F}^{t} fN(t)E(t)dt \quad \text{for} \quad t_F < t \leqslant t_\lambda$$
$$A_m = A(t_\lambda)$$

where f is a positive factor of proportionality.

For legal minimum length l_R corresponding to age t_R, the proportion of the maximum egg production per recruit, $\bar{E}(t_R,P)$, is given by:

$$(2)\quad \bar{E}(t_R,P) = \left\{\int_{t_R}^{\min(t_\lambda,t_R+P)} A_t dt\right\}/PA_m$$

A computer program produced tables (t_R by P) of $\bar{B}$ and $\bar{E}$ as percentages of maximum biomass and egg production for any set of input parameters L_∞, K, M, t_λ, t_F, e_1, and e_2. Note that a value of f is unnecessary because it appears as a multiplier of both the numerator and denominator of equation (2). The relationships above were programmed as explicit FORTRAN functions, which were then integrated by a commercially available numerical integration procedure which uses the Romberg method.

It is important to understand the way in which increased effort by divers is manifested in the abalone fishery. Because area of bottom on which abalone are found is limited, if divers spend more days per year fishing, some areas will be visited more often and the period between visits to substocks will decrease. In the extreme, a reef would be fished clear of all recruits as soon as they appeared ($P=0$), so that each individual would be captured as soon as it reached l_R.

Population parameters have been estimated by tagging studies and size frequency analyses (Shepherd and Hearn 1983; Shepherd et al. 1982). Parameters for each of the ten substocks into which the fishery was subdivided are shown in Table 1 (S.A. Shepherd, Dep. of Fisheries, Box 1625, Adelaide, 5001, Australia, unpublished data). Figure 2 shows the relationship amongst age t, weight $w(t)$, and fecundity $E(t)$ for greenlip abalone in area W3. S.A. Shepherd (unpublished data) has found that abalone exhibit aggregating behaviour after they reach about 4 yr, suggesting that abalone younger than this contribute little to fertile egg production and subsequent recruitments. The effects of varying t_F were investigated by setting $t_F=3$ and 4 yr.

The model is relatively insensitive to the assumption that all abalone over the legal length are removed during a visit by divers. A factor c can be defined as the constant proportion of all age-classes available for exploitation which are removed in an intensive fishing visit. All the model runs in this study assumed that $c=1.0$. However, the model can be extended to deal with the case where c is less than one. For example, $\bar{B}(t_R,P)$ would become $c\bar{B}(t_R,P) + c(1-c)\bar{B}(t_R,2P) +$

$c(1-c)^2\bar{B}(t_R,3P) + \ldots$

For an extreme value of $c=0.8$, the first three coefficients of the $\bar{B}$ factors are 0.8, 0.16, and 0.032, showing that the first term of the summation is dominant, with the second contributing slightly. The actual figures presented in the tables below (Tables 2 and 3) show that the results of the study do not depend critically on $c=1.0$, thus confirming the initial assumption.

Results

The model was run for each of the 10 substocks in Table 1 over ranges of legal minimum lengths l_R and

TABLE 1. Population dynamics parameters for greenlip abalone *Haliotis laevigata* (G) and blacklip abalone *H. rubra* (B) at various areas in South Australia as estimated by S. A. Shepherd. The relative importance of a species at an area is represented by the average annual catch (tonnes meat wt) from 1980/81 to 1982/83. L_∞ and K are von Bertalanffy growth parameters, M is the instantaneous natural mortality rate, a and b relate weight (g) to length (mm), t_m is the age at maximum biomass and the parameters t_F (calculated age at first fecundity), e_1 and e_2 determine fecundity (millions of eggs) from weight.

Area	Sp.	Catch (t)	L_∞ (mm)	K (/yr)	M (/yr)	$a/10^{-5}$	b	t_m (yr)	t_F (yr)	$e_1/10^{-2}$	e_2
W1	G	18.2	140	0.40	0.22	1.75	3.41	4.66	1.53	1.51	0.381
	B	14.0	143	0.32	0.21	1.75	3.41	5.37	1.85	1.51	0.381
W2	G	38.1	160	0.60	0.22	10.0	3.15	3.70	2.07	1.43	4.280
	B	34.7	144	0.40	0.21	1.75	3.41	4.76	1.47	1.51	0.381
W3	G	77.8	150	0.60	0.22	10.0	3.15	3.70	2.37	1.43	4.280
	B	55.2	144	0.40	0.21	1.75	3.41	4.76	1.47	1.51	0.381
C	G	50.2	140	0.50	0.22	1.75	3.41	4.11	1.22	1.51	0.381
	B	6.5	143	0.32	0.21	1.75	3.41	5.37	1.85	1.51	0.381
S	G	0.9	140	0.50	0.22	1.75	3.41	4.11	1.22	1.51	0.381
	B	34.5	155	0.25	0.21	1.75	3.41	6.08	2.13	1.51	0.381

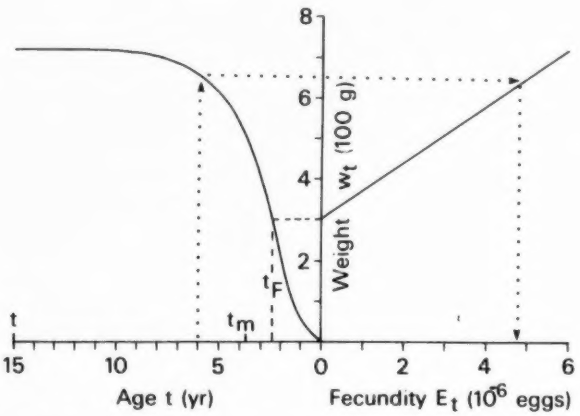

FIG. 2. Relationship amongst age (t), weight $w(t)$, and fecundity $E(t)$ (see arrows) for greenlip abalone in area W3. The latter is represented as the number of eggs carried by an individual of given weight in the spawning season. t_m is the age of maximum biomass of an age-class, while t_F is the calculated age at first fecundity.

periods P between fishing visits to substocks and the results shown in Table 2.

Interpretation of the results is illustrated for the most productive single area (W3). For greenlip abalone, the range of values of l_R and P over which long-term biomass yield per recruit is more than 90% is large, showing the relative insensitivity of yield to changes in these control variables. Continuous fishing with very high fishing intensity is modelled by $P=0$ and examination of this column reveals that 100% yield is obtained at $l_R=135$ mm and its immediate vicinity, which corresponds to $t_R=3.8$ yr which, as expected, includes $t_m=3.7$ yr. For l_R's less than 135 mm, the yield first increases as P increases, as more abalone reach their maximum potential biomass, and then decreases due to the effects of natural mortality. For l_R's greater than 135 mm, an increase in P results in lower yields, because the age at maximum efficiency has been exceeded. Because blacklip abalone in area W3 are slower growing and reach a smaller size, maximum yield is achieved at lower values of l_R.

Egg production per recruit increases when abalone are allowed more time to spawn, either by increasing P through longer rests between fishing visits, or through protection over a longer portion of their lives by increasing l_R.

Comparison of the estimates of efficiency in Table 2 shows that egg production is much more sensitive to input parameter values and exploitation controls than is biomass yield. The latter, in fact, displays remarkable stability, remaining above 90% for large ranges of controls. Egg production is not so stable. There are large differences between areas and species. The percentages also respond much more significantly to changes in controls, particularly where the figures are low. For example, for greenlip abalone in area W2 ($t_F=3$ yr), closures of 2 yr result in increases in egg production orders of magnitude greater than those from continuous fishing ($P=0$ yr) at $l_R<135$ mm.

Sluczanowski (1984) showed that the age at first effective fecundity t_F was the parameter to which the model was most sensitive. The extent of this sensitivity is illustrated in Table 3, which compares egg production in area W3 for both species for $t_F=2.37$ (age where $E(t)$ crosses the axis in Fig. 2), 3.0 and 4.0. The effects of egg production on subsequent recruitment to the fishery are mainly speculative, but the potentially serious consequences for future recruitment of t_F being large are such that it indicates a priority area for further biological research. For example, for the present $l_R=130$ mm, the model shows that there is a 12-fold difference in egg production in greenlip abalone at area W3 for all substocks visited more than once per year depending on whether $t_F=2.37$ or 4.00 yr. The reason for this sensitivity is clear from examining the ages corresponding to various values of l_R: fast growing animals spend a much shorter time growing from t_F to t_R, therefore having less opportunity to produce eggs.

To allow comparison of the effects of various management strategies, the disaggregate results presented in Table 2 were summed to produce

TABLE 2. The effects of combinations of legal minimum length (l_R) and period between intensive fishing visits (P) on biomass yield per recruit and egg production per recruit for abalone in substocks described in Table 1 by area and species (G = Greenlip, B = Blacklip). The age at first fecundity t_f was assumed to be 3 yr and the relative importance of each sub-table is represented by its 3 yr average catch (t) in its top left corner.

				Biomass						Eggs($t_f = 3$)					
		Age(yr)		Greenlip period (yr)			Blacklip period (yr)			Greenlip period (yr)			Blacklip period (yr)		
Area	l_R (mm)	G	B	0	1	2	0	1	2	0	1	2	0	1	2
				18			14			18			14		
W1	120	4.9	5.7	100	99	96	100	99	96	22	28	35	27	33	39
	125	5.6	6.5	98	95	90	98	95	90	31	38	44	36	42	48
	130	6.6	7.5	90	85	79	91	86	81	44	50	56	48	54	59
	135	8.3	9.0	70	64	59	75	70	64	64	68	72	64	69	73
	140		12.1	0	0	0	45	41	37	100	100	100	87	90	92
				38			35			38			35		
W2	120	2.3	4.5	79	91	95	99	100	98	0	1	5	16	23	29
	125	2.5	5.1	85	94	97	100	99	95	0	2	7	24	30	37
	130	2.8	5.8	91	97	98	98	94	89	0	4	10	34	40	46
	135	3.1	6.9	96	99	97	88	83	77	1	7	14	47	53	58
	140	3.5	9.0	99	99	96	65	60	55	5	12	20	68	72	76
	145	4.0		100	97	92	0	0	0	12	19	27	100	100	100
				78			55			78			55		
W3	120	2.7	4.5	89	96	97	99	100	98	0	2	8	16	23	29
	125	3.0	5.1	95	99	98	100	99	95	0	5	12	24	30	37
	130	3.4	5.8	99	99	96	98	94	89	3	10	17	34	40	46
	135	3.8	6.9	100	98	93	88	83	77	9	16	24	47	53	58
	140	4.5	9.0	97	92	85	65	60	55	19	26	33	68	72	76
	145	5.7		84	77	71	0	0	0	36	42	49	100	100	100
				50			7			50			7		
C	120	3.9	5.7	99	100	97	100	99	96	12	19	26	27	33	39
	125	4.5	6.5	100	98	93	98	95	90	20	27	34	36	42	48
	130	5.3	7.5	96	91	85	91	86	81	32	39	45	48	54	59
	135	6.7	9.0	80	74	68	75	70	64	50	56	61	64	69	73
	140		12.1	0	0	0	45	41	37	100	100	100	87	90	92
				1			35			1			35		
S	120	3.9	6.0	99	100	97	100	100	99	12	19	26	25	30	36
	125	4.5	6.6	100	98	93	100	99	97	20	27	34	32	37	43
	130	5.3	7.3	96	91	85	99	96	92	32	39	45	40	46	51
	135	6.7	8.2	80	74	68	93	89	84	50	56	61	50	55	60
	140		9.3	0	0	0	83	78	73	100	100	100	62	67	71
	145		11.0	0	0	0	66	61	57	100	100	100	77	80	84

aggregate figures. Average catches over the past three years provide a measure of the relative importance of sections of the stock and were used as weighting factors. To estimate, for example, the effects on egg production of both species combined in area W3 ($l_R = 130$ mm, $P = 1$ yr, $t_f = 3$ yr), the following formula would be used:

$$\text{Eggs (both sp)} = (\text{Gr. eggs} \times \text{catch} + \text{Bl. eggs} \times \text{catch}) / \text{total catch}$$

$$22 = (10 \times 78 + 40 \times 55)/(78 + 55)$$

A consequence of such aggregation is that while it may be possible to maximize egg or biomass production for an area or species separately, common management controls produce compromises which often prevent achievement of these maxima.

Tables similar to Table 2 were produced which contained analogous figures for combined areas, combined zones and combined species. They were made available to fisheries managers and used to determine management strategies. Figure 3 is a graphical presentation of the results for both species over the state. Note that although egg production appears to be above 20% for all periods providing $l_R > 130$ mm, the disaggregated information contained in Table 2, that egg levels for greenlip abalone in area W2 are very low, is obscured.

To model the consequences of no closures being applied, the period between intensive fishing visits P was chosen as 0.5 yr. This choice was based on the assumption that, in the long-term, the competitiveness and increased efficiency of divers will be such that most abalone will survive about half a year after reaching

TABLE 3. The effects of different values of age at first effective fecundity (t_f) on egg production of both abalone species in area W3. Three values of t_f were used: that calculated assuming all eggs are fecund ($t_f = 2.37$, see Table 1), and $t_f = 3$ and 4 yr.

Legal mins		Egg production (% of maximum possible)											
		($t_f = 2.37$) Period (yr)				($t_f = 3$) Period (yr)				($t_f = 4$) Period (yr)			
l_R (mm)	t_R (yr)	0	1	2	3	0	1	2	3	0	1	2	3
Greenlip abalone (*Haliotis laevigata*)													
120	2.68	1	4	10	17	0	2	8	15	0	0	2	8
125	2.99	3	8	14	21	0	5	12	19	0	0	4	11
130	3.36	6	12	19	26	3	10	17	24	0	1	8	15
135	3.84	12	18	26	32	9	16	24	31	0	6	14	22
140	4.51	21	28	35	41	19	26	33	40	8	17	25	32
145	5.67	37	44	50	55	36	42	49	54	27	35	42	48
Blacklip abalone (*H. rubra*)													
120	4.48	21	27	34	39	16	23	29	35	7	14	21	28
125	5.06	28	35	40	46	24	30	37	42	15	22	29	36
130	5.83	38	44	49	54	34	40	46	51	26	33	40	46
135	6.93	51	56	61	65	47	53	58	63	41	48	53	59
140	8.96	70	74	78	81	68	72	76	79	65	69	73	77

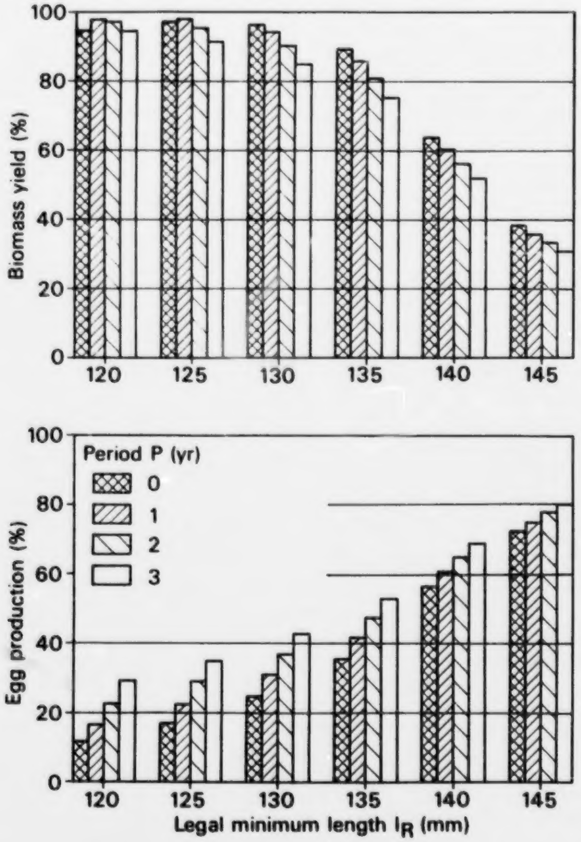

FIG. 3. The efficiency of biomass yield per recruit and egg production per recruit for both abalone species in South Australia as functions of the legal minimum length (l_R) and the period between intensive fishing visits (P).

their legal recruitment size l_R. The results, including aggregate estimates for zone *W* and the state (SA) are shown in Table 4. The fact that greenlip stocks in areas W2 and W3 probably require larger size limits than other substocks is immediately apparent.

Tables 2 and 4 and the aggregated estimates derived from them were used to determine management strategies. In choosing these, a number of compromises were made which balance potential profitability, the relative risk to stock survival through reduced egg production and the feasibility and costs of administration and enforcement. The longstanding situation of a uniform size limit for both species over all zones and no closures is the simplest to administer and police, because differential size limits between zones and selective area closures bring difficulties such as the necessity to resolve conflicting commercial and recreational interests, publicity and extension and more complex legal proceedings associated with prosecutions.

Table 5 compares eight possible management strategies, ranging from the current simple one, to a complex combination of area specific closures and size limits. Any algorithm for determining an optimal strategy depends on precise specification of an objective function and set of constraints. The procedures used to construct Table 5 were more subjective, particularly with regard to minimum levels of egg production, which were arbitrarily chosen following discussions between biologists and divers. Guided by a set of rudimentary rules, the set of alternatives were chosen taking into account the likely concerns of both industry and administrators. For example, two open areas in the same zone could not have different size limits for a species. Management constraints adopted included: ensure that average egg production exceeded 20% (riskier) or 30% (safer) and then maximize yield per recruit and egg production, and closures in an area must apply to both species simultaneously.

Although it is the simplest regime to administer, the present management arrangement (Strategy 1) has the obvious shortcoming that a large proportion of stocks are in low egg production categories (stocks producing 116 t/yr have egg production below 10%.) Setting statewide separate legal minimum lengths for the two species under a "risky" regime (Strategy 2), nevertheless reduces the amount of stock producing less than 10% of eggs to 38 t/yr. Alternatively, a "safer" equivalent policy (Strategy 3) reduces biomass yield but gives an even higher egg production. However the biomass yield of zone C would be unacceptable to industry and managers.

Strategies involving different size limits for the same species in different zones are more difficult to administer, but offer substantial benefits. Strategy 4, which is of this type, follows suggestions made by divers and its only shortcoming is in reducing biomass yield by 8% below the current level due mainly to the poor performance for greenlip abalone in area W1. Strat-

TABLE 4. The effects of legal minimum length l_R on abalone yield per recruit (as % of possible maximum) and category of egg production for various areas under a no closure policy ($P=0.5$ yr). The catches (t) indicate the relative importance of each column. The production of eggs is given by the following key: ** = 0-9.9%, * = 10-19.9%, + = 20-29.9%, − = 30-49.9%, . = 50-100%.

l_R(mm)	W1	W2	W3	W	C	S	SA
Greenlip							
Catches =	18	38	78	134	50	1	185
120	100+	85**	93**	91**	100*	100*	94**
125	97−	90**	97**	95**	99+	99+	96*
130	88−	94**	99**	96*	94−	94−	95*
135	67.	98**	99*	94*	77.	77.	90*
140	0.	99**	95+	83+	0.	0.	60−
145	0.	99*	81−	75−	0.	0.	54.
Blacklip							
Catches =	14	35	55	104	7	35	146
120	100−	100+	100+	100+	100−	100+	100+
125	97−	100+	100+	99+	97−	100−	99−
130	89.	96−	96−	95−	89.	98−	95−
135	73.	86.	86.	84.	73.	91.	85.
140	43.	63.	63.	60.	43.	81.	64.
145	0.	0.	0.	0.	0.	64.	15.
Both species							
Catches =	32	73	133	238	57	36	331
120	100+	92*	95**	95*	100*	100+	96*
125	97−	94*	98*	97*	99+	99−	97+
130	88−	95*	98*	96+	93−	97−	95+
135	69.	92+	93+	90−	76.	91.	88−
140	19.	82−	81−	73−	5.	78.	62.
145	0.	51.	47.	42.	0.	62.	37.

TABLE 5. A comparison of alternative management strategies for the South Australian abalone fishery involving different combinations of minimum length l_R and closures of zone W (yr). Each pair of figures in the "Biomass, Egg" section of the table represents the biomass yield and egg production per recruit expressed as a % of the maximum possible for that area. The bottom part of the table shows the annual catches of substocks in various egg production categories.

	Strategy:	1		2		3		4		5		6		7		8	
	Zone W closure:	—		—		—		—		—		1 yr		2 yr		2 yr	
	Area of regulation:	state		state		state		zone		area		zone		zone		area	
	Recruitment risk:	risky		risky		safer		safer		safer		safer		safer		risky	
	Administration:	simple		simple		simple		hard		imprac.		hard		hard		imprac.	
l_R	W1 G,B:	130	130	135	120	140	125	145	130	125	125	145	130	145	130	120	120
	W2 G,B:	"	"	"	"	"	"	"	"	145	130	"	"	"	"	145	125
	W3 G,B:	"	"	"	"	"	"	"	"	"	"	"	"	"	"	140	"
	C G,B:	"	"	"	"	"	"	130	"	130	125	130	"	130	"	125	120
	S G,B:	"	"	"	"	"	"	"	125	"	"	"	125	"	125	"	125
Biomass, Eggs	W:	96	23	97	19	90	29	84	40	92	34	81	43	76	49	91	34
	C:	93	37	80	50	12	93	93	38	94	36	93	38	93	38	99	25
	S:	97	43	99	29	97	37	100	35	100	35	100	35	100	35	100	35
	SA:	95	28	94	25	77	41	87	39	93	34	85	41	82	46	93	33
Tns caught per yr where egg production is below %'s.	<10%:	116		38		38		0		0		0		0		0	
	<20%:	116		206		38		38		38		38		0		0	
	<30%:	116		262		206		38		331		38		38		96	
	<50%:	310		262		262		292		331		292		292		331	

egy 5, which uses area specific size limits to allow all areas in zone W to realize high biomass yield takes this into account, but appears to be administratively impractical.

Divers in zone W have also expressed interest in the value of closures. Strategies 6 and 7 show how Strategy 4 can be extended to include one or two year closures. The long-term biomass yield per recruit falls in zone W, while egg production improves. Once again, special provision for area W1, modelled in strategy 8, would allow better yields.

In summary, comparison of the range of strategies demonstrates that the fishery can be tuned closer to ones objectives, but only with more complex controls. The degree to which this is done will depend on a subjective balance of the relative importance of yield, egg production and costs.

Discussion

Estimates of yield and egg production per recruit using various management strategies involving legal minimum lengths and closures can be obtained from this model and are summarized in Tables 2 to 5. Under equilibrium conditions, the rate of production of biomass from a stock (kg per yr) is equal to the product of two terms: the yield per recruit (kg per recruit) and the rate of arrival of recruits to the fishery at length l_R (recruits per yr). The effects of combinations of l_R and P on yield per recruit are apparent from direct inspection of the tables above. However, the relationship between egg production and subsequent recruitment is more speculative and deserves further discussion.

The concept of "recruitment overfishing" is well recognized in fisheries management (Cushing 1977). A number of sedentary mollusc stocks, including abalone, around the world have suffered collapses in recruitment to very low levels, probably as a result of heavy fishing pressure (Breen 1980; Cicin-Sain et al. 1977; Fedorenko and Sprout 1982; Sainsbury 1982). The evidence from a number of abalone substocks in South Australia which have never recovered after intensive fishing also casts doubts on the supposed resilience of species whose members are each capable of shedding millions of eggs.

In the absence of firm evidence of a direct relationship between egg production and subsequent recruitment to the fishery, for what level should managers aim? The fact that a number of fisheries have collapsed suggests caution in dealing with reproductive factors such as egg production. Abalone probably evolved producing a large number of eggs in order to deal with environmental risk. A fishing strategy which reduces egg production by orders of magnitude probably increases the chances that a substock will be unable to survive stresses such as temperature and current changes, which previously it could. The possibility of a link between egg production and subsequent recruitment is suggested by examination of the tables for greenlip abalone in areas W2 and W3 which show low levels of egg production resulting from current management strategy. These are precisely the substocks in which instances of nonrecovery have been reported.

Data collected over 13 yr at an isolated substock by S. A. Shepherd show a positive correlation between the biomass of abalone over 4 yr old and subsequent recruitment of 1 yr olds. Since abalone younger than 4 yr produce relatively few eggs, it follows that future recruitment may in reality be determined by the level of egg production.

In summary then, the purpose of trying to maintain high levels of egg production are twofold: (1) to improve the security of the stock in the short- to medium-term and (2), perhaps, to increase productivity in the long-term. Whilst the latter is by no means established for South Australia, fisheries managers cannot afford to take chances with the former.

This study facilitates a rational choice of management strategies for the South Australian abalone fishery, as well as suggesting directions for future research. In particular, it has enabled me to demonstrate a potential threat to future recruitment through the combined effects of increasing effort and the retention of current size limits. An increase in l_R in zone W from 130 to 145 mm would significantly reduce this risk, but at the expense of a slight drop in biomass yield per recruit in area W1. (Since the population parameters for area W1 were inferred from studies carried out at other areas judged to be similar, projected yield foregone may not be as significant as implied in these calculations). Closures could be introduced to complement the change in size limit, and, as well as increasing egg production, would also offer the divers potential improvements in profitability.

Divers in zone S have suggested the existence of significant blacklip abalone stocks whose members they believe rarely attain the upper length limit estimate L_∞ used above. This species is more cryptic than greenlip abalone and there have been no reports of recruitment collapses locally, or in similar stocks in Victoria, an adjacent state where the width limit for an extension of the same stock corresponds to a length limit of about 120 mm. Reduction of the blacklip size limit to 120 mm would probably not put the stock at risk, while at the same time would raise the long-term biomass yield per recruit and potentially free new stocks for exploitation.

The wide range of values in egg production indicates its sensitivity to changes in l_R, P and choice of parameters. If this reflects the real situation, the model demonstrates the importance of protection of parental stocks for long-term security of recruitment. A number of critical events occur to an abalone within a relatively short period of growth: its fecundity increases rapidly, it starts to exhibit aggregating behaviour, its year-class reaches its maximum biomass, and the individuals become more liable to capture by increasing fishing effort. Further biological research to establish more accurately the population parameters describing these processes is important.

This study has shown that a model based on population parameters which are easier to estimate than fishing mortality (F) can provide useful guidance to managers, and the way in which it can guide management in resolving conflicting objectives has been demonstrated by a case study. It should also be possible to apply it to other sedentary stocks which are also fished periodically and where a high proportion of the available age-classes are harvested at each visit.

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An Invertebrate Resource Survey of Lingayen Gulf, Philippines

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LOPEZ, M. D. G. 1986. An invertebrate resource survey of Lingayen Gulf, Philippines, p. 402–409. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

The annual invertebrate catch from Lingayen Gulf, a major fishing ground, was estimated from recall interviews and port sampling. Over 120 species are taken from the Gulf, with approximate annual catches of 2800 t. About 52% of landings consist of species hand-gathered from shallow water while 46% is taken with small-scale gear; only 2% is landed by a 14-trawler commercial fleet.

The average yield rate to the small-scale fisheries as a whole would be about 3 t·km^{-2}·yr^{-1} within the 37-m isobath, while that for hand-gathered species alone would be about 25 t·km^{-2}·yr^{-1} within the 2-m isobath.

The survey method and the quality of data collected reflect logistic constraints on monitoring of artisanal fisheries in general. However, it is a fast, inexpensive means of obtaining baseline information which presently is not available.

Because nearshore fisheries utilize a wide array of gears to take a diverse catch landed throughout the coast, it is difficult to impose catch quotas and size limits. Management measures may best be implemented with granting territorial use rights at the village level under the supervision of fishery officers. Existing stock assessment models do not appear to be of practical use in Philippine fisheries because stock interactions are not well accounted for.

L'auteur a estimé la prise annuelle d'invertébrés dans le golfe de Lingayen, un banc de pêche important, à partir d'entrevues mémoires et d'échantillonnages au port. Plus de 120 espèces sont tirées de ce Golfe pour des prises annuelles d'environ 2 800 t. Environ 52 % des quantités débarquées se composent d'espèces cueillies à la main dans des eaux peu profondes tandis que 46 % sont pris au moyen de petits engins de pêche; 2 % seulement sont débarqués par une flotte commerciale de 14 chalutiers.

Le taux de rendement moyen par rapport à la pêche à petite échelle dans son ensemble serait d'environ 3 t·km^{-2}·an^{-1} jusqu'à l'isobathe de 37 m, tandis que celui des seules espèces cueillies à la main serait d'environ 25 t·km^{-2}·an^{-1} jusqu'à l'isobathe de 2 m.

La méthode de relevé et la qualité des données recueillies reflètent les contraintes logistiques sur le contrôle de la pêche artisanale dans son ensemble. Ce sont toutefois des moyens à la fois rapides et peu coûteux pour obtenir des informations de base qui font actuellement défaut.

Comme la pêche pratiquée près de la côte fait appel à un vaste réseau d'engins pour obtenir une prise variée qui est débarquée sur toute la côte, il est difficile d'imposer des contingentements de prises et des limites de tailles. La meilleure façon de mettre en œuvre des mesures de gestion consiste à accorder des droits d'exploitation territoriale à l'échelon du village sous la supervision d'agents des pêches. Les modèles d'évaluation des stocks qui existent actuellement aux Philippines ne semblent pas pratiques d'utilisation parce que les interactions de stocks ne sont pas bien représentées.

Introduction

The marine invertebrate fisheries of the Philippines involve a large number of species, mostly of low economic value, that are mainly landed by the municipal fishery sector. Presidential Decree No. 704 (Fisheries Decree of 1975) defines municipal fishing as fishing using boats of 3 gross tons or less, or using gear not requiring the use of boats, within 3 nautical miles (5.6 km) from shore. This is opposed to commercial fishing which is conducted in water over 7 fathoms (12.8 m) deep using boats over 3 gross tons. Monitoring of municipal catches from various fishing grounds began in 1976 and among invertebrates, only covers crustaceans, although yields of molluscs and echinoderms are known to be substantial in many areas. Because landing sites for the municipal fisheries are dispersed throughout the country's extensive coastline, catch estimates for this sector are acknowledged to be too low, with unknown confidence limits.

Continued growth in the number of fishermen, partly through displacement of labor from agriculture and industry and the provision of subsidies for fishing boats and gear, and a general acceleration of coastal development have raised concern about possible effects on the fishery yields from Lingayen Gulf, a major fishing ground on the west coast of Luzon Island. In 1983, the Philippine Council for Agriculture and Resources Research and Development (PCARRD) commissioned the Bureau of Fisheries and Aquatic Resources (BFAR), the University of the Philippines in the Visayas Institute of Fisheries Development and Research (UPV-IFDR), and the University of the Philippines Marine Science Institute (UPMSI) to conduct a preliminary survey of the Gulf to determine catch composition, estimate total catches especially in the municipal sector, and identify species for which funds for biological studies should be allocated. Oceanographic observations were conducted by the BFAR, while fish catches were monitored in commercial and municipal fisheries by the UPV-IFDR. Seaweed and invertebrate harvesting, the latter being the subject of this paper, were covered by the UPMSI with the cooperation of the UPV-IFDR.

Lingayen Gulf (Fig. 1) opens north into the South China Sea, enclosing an area of approximately 2000 km^2. The mouth is about 50 km across from Cape Bolinao in the west to Poro Point in the east. The coastline between these two points is roughly 160 km. The western fringes of the gulf are largely coralline while the south and east coasts, to which nearshore trawling is confined, are sandy and muddy. Maximum charted depths within the Gulf are about 110 m.

The southwest monsoon affects the Gulf from July to October, with typhoons prevalent from mid-September to the end of October (Sebastian et al. 1959). The Gulf waters are warm, averaging 26–31°C at the surface and 24–29°C at the bottom during the annual cycle. Mean monthly salinity ranges from 25 to 35 ppt at the surface and 27–35 ppt at the bottom, with estuarine conditions prevailing along the south and southeast coasts (Estudillo et al. 1985).

Official Reported Catches

Table 1 shows invertebrate catch data for the Gulf from 1976 to 1981. Commercial catches from deeper portions of the Gulf consist mainly of shrimps, prawns and squid. From an apparent peak of 83 t in 1976, the shrimp and prawn catch decreased to 13 t in 1981. Shrimps, prawns and squid accounted for only 2.3% of total commercial catches in 1981.

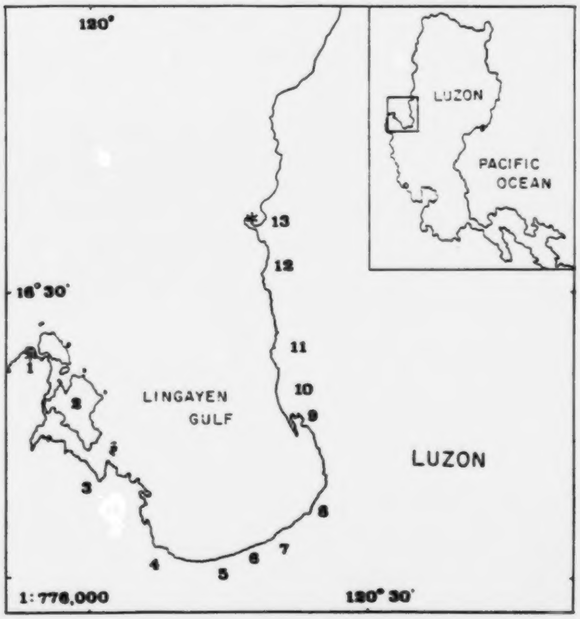

FIG. 1. Location of Lingayen Gulf in the Philippines, with the location of sites mentioned in the text (1 — Bolinao, * — Cape Bolinao, 2 — Anda, 3 — Alaminos, 4 — Labrador, 5 — Lingayen, 6 — Binmaley, 7 — Dagupan, 8 — San Fabian, 9 — Santo Tomas, 10 — Agoo, 11 — Aringay, 12 — Bauang, 13 — San Fernando, * — Poro Point).

The bulk of the invertebrate catch, averaging about 88% of reported catches from 1976 to 1981, is landed by municipal fishermen. Catches of less valuable species groups, mainly non-cephalopod molluscs and echinoderms taken by hand, are generally not quantified in official statistics.

Study Estimated Catches

Information on seasonal availability of each species, prices, gear, and estimates of catch per unit effort and number of fishermen per village were obtained from fishermen and vendors. Total invertebrate catches were estimated from port sample and gear census data obtained by UPV-IFDR and BFAR teams in the nine major fishing towns around the Gulf, and from recall interviews, especially on gleaning, conducted by the UPMSI team in 55 villages. These estimates of annual catches from the Gulf were made with the following assumptions:

1) The annual fishing season lasts about 180 d, with peak catches within a 120-d period (Latorre et al. 1980).

2) Catches outside the fishing season are negligible.

3) Catches from areas not covered in the survey are negligible.

4) The 14 commercial trawlers operating within the Gulf make 100 trips per year while municipal trawlers numbering about 300 make 150 trips per year (Prof. A. Mines, UPV-IFDR, pers. comm.).

5) Quantity of each species group landed by each gear type in a given locality averaged over the period for which data are available are representative of the catch through the fishing season.

Results

Species — At least 128 species are commonly taken by municipal fishermen, including 10 crabs, 4 lobsters, 9 shrimps and prawns, 46 gastropods, 42 bivalves, 8 cephalopods, 7 sea cucumbers, and 2 sea urchins (Table 2). A few other edible species of highly localized use are collected mainly for household consumption by children, while a wide variety of specimen shells comprise a minor by-catch of reef gleaners, divers, and trawlers.

Shelled molluscs, the largest species group, are mostly gathered by hand in shallow water, especially from reefs off the west coast. Most species are edible while a few are gathered in large quantities for shellcraft, especially at Bolinao and Anda where these species comprise 66 and 82%, respectively, of harvested species.

Crustaceans are the main invertebrate catch on the south coast where the bottom is sand and mud, and where large sections of the coast are estuarine.

The nearshore invertebrate fisheries of the east coast are not as significant as those of the west and south. Except for scallops taken off the inner section of the

TABLE 1. Invertebrate catch (t and percent in total catch) from Lingayen Gulf, 1976–81. (Source: *Fisheries Statistics of the Philippines*, 1976–81, BFAR, Manila.)

ISSCAAP[a] Group	1976	1977	1978	1979	1980	1981
A. Crabs:						
Commercial	—[b]	—	1	—	—	—
Municipal	156	21	60	306	128	61
Lobsters:						
Municipal	5	—	1	2	4	24
Shrimps and Prawns:						
Commercial	83	58	51	82	19	13
Municipal	772	174	208	222	1704	313
Miscellaneous Marine Crustacea[c]:						
Commercial	—	—	4	—	—	—
Municipal	—	16	—	41	—	1
Scallops:						
Commercial	—	—	6	—	—	—
Other Bivalves[d]:						
Municipal	5	—	—	—	62	10
Squid, Cuttlefish, and Octopus:						
Commercial	16	56	56	77	34	29
Municipal	356	116	249	316	307	684
Others[e]:						
Municipal	3	1	—	—	—	—
Total Invertebrate Catch:						
Commercial	99	114	118	159	53	42
Municipal	1297	328	524	887	2205	1093
	1396	442	642	1046	2258	1135
Total Fish Catch:						
Commercial	1350	1946	1915	1891	1338	1842
Municipal	10667	5554	4445	6281	3149	3965
	12017	7500	6360	8172	4487	5807
Total Catch:	13413	7942	7002	9218	6745	6942
B. Percent invertebrates in total catch:						
Commercial	6.8	5.5	5.8	7.8	3.8	2.2
Municipal	10.8	5.6	10.5	12.4	41.2	21.6

[a] International Standard System for Classification of Aquatic Animals and Plants.
[b] Indicates negligible catches.
[c] Includes only mantis shrimp.
[d] Includes only Tridacnidae and *Placuna placenta*.
[e] Includes only sea urchins and sea cucumbers.

east coast, which may occasionally comprise a sizeable portion of the invertebrate catch of small trawlers, only small quantities of a few species are taken from this area. The catch of specimen shells is diverse but meager. Most invertebrates marketed along the east coast are brought in from the west coast and even from Manila Bay, or are cultured in ponds.

Fishing methods and landings by gear type — Commercial fishing vessels, which are prohibited from operating within 13 km (7 nautical miles) of shore, are equipped with otter trawls. Municipal fishermen, on the other hand, utilize a wide variety of mobile and stationary gear, shifting gear types and fishing grounds according to species availability. On the west coast, fish traps, spears and surface gill nets are most commonly used. Small trawls, beach seines and lift nets are prevalent in the south, and round haul seines in the east (Ferrer et al. 1985).

The average catch composition from commercial and small-scale gear based on port sampling is shown in Table 3. Fish comprise over 50% of the catch of all gear except lift nets and small (municipal) trawls where shrimp predominate. Total commercial trawl catches are much higher than those from municipal trawls although on average both gear types take approximately the same weight of invertebrates per day. Species composition of the invertebrate catch also differs, scallops and squid comprising most of commercial catches, while shrimp and smaller amounts of scallops are taken with municipal trawls which operate in shallower water.

Lift net and fish pen invertebrate catches consist

TABLE 2. Exploited invertebrate species in the Lingayen Gulf, and average CPUE (catch (kg) per day) of hand-gathered species in 1983 based on recall interviews. * = incidental.

Crabs:

Calappa sp.
Charybdis feriata
Matuta lunaris
Podophthalmus vigil
Portunus pelagicus
Portunus sanguinolentus
Scylla serrata
Thalamita crenata
Varuna litterata
Thalassina anomala

Lobsters:

Panulirus ornatus
Panulirus penicillatus
Panulirus versicolor
Parribacus caledonicus

Shrimps and prawns:

Marcobrachium lar
Metapenaeus endeavouri
Metapenaeus ensis
Trachypenaeus fulvus
Penaeus canaliculatus
Penaeus incisipes
Penaeus monodon
Acetes sp.

Miscellaneous Marine Crustacea:

Squilla nepa

Gastropods:

	CPUE (kg·d^{-1})		(CPUE (kg·d^{-1})
Astraea calcar	*	*Natica sagittata*	1
Clypeomorus		*Nerita chamaeleon*	1
batillariaeformis	10	*Nerita turrita*	1
Conus coronatus	*	*Oliva tricolor*	*
Conus flavidus	*	*Potamides pyriformis*	1
Conus lividus	*	*Pyrene versicolor*	1-10
Conus quercinus	*	*Rhinoclavis vertagus*	2
Conus suratensis	*	*Strombus dentatus*	*
Cymatium muricinum	10	*Strombus floridus*	—
Cymbiola vespertilio	*	*Strombus gibberulus*	*
Cypraea annulus	1-10	*Strombus luhuanus*	3-10
Cypraea arabica	1	*Strombus mutabilis*	*
Cypraea mappa	1	*Strombus urceus*	5-100
Cypraea moneta	1-10	*Tectus fenestratus*	*
Cypraea talpa	1	*Tectus pyramis*	*
Cypraea tigris	*	*Tibia fusus*	*
Fasciolaria filamentosa	*	*Tonna allium*	*
Fasciolaria gigantea	*	*Tonna sulcosa*	*
Fasciolaria trapezium	1-5	*Trochus maculatus*	*
Haliotis asinnina	1	*Trochus niloticus*	*
Lambis lambis	2	*Trochus obeliscus*	*
Melanoides sp.	—	*Turitella terebra*	30
Murex ternispina	*	*Xenophora solaris*	*
Nassarius coronatus	1		

Bivalves:

Amusium		*Lima vulgaris*	*
pleuronectes	5-20	*Malleus malleus*	*
Anadara antiquata	5-15	*Marcia hiantina*	10
Anadara granosa	5	*Marcia japonica*	1
Anadara pilula	*	*Marcia marmorata*	1-5
Anadara truncata	5	*Modiolus philippinarum*	10
Anomalodiscus		*Paphia striata*	1
squamosus	1-15	*Pinctada fucata*	2
Asaphis dichotoma	5	*Pinctada maxima*	2
Atrina vexillum	*	*Pitar striatum*	2-10
Callista brevisiphonata	*	*Placuna placenta*	15
Cardium subrugosum	5-15	*Quidnipagus palatam*	*
Circe scripta	1	*Soletellina elongata*	10
Codakia tigerina	1	*Soletellina minor*	5-15
Corbicula fluminea	—	*Spondylus squamosus*	*
Crassostrea iredalei	20-200	*Tellinella staurella*	0.5
Crassostrea		*Trachycardium*	
malabonensis	20-200	*variegatum*	1
Crassostrea		*Tridacna maxima*	5
palmipes	20-200	*Tridacna squamosa*	5
Ctena divergens	*	*Venus alta*	*
Cyrena ventricosa	*	*Venus clathrata*	1
Donax radians	5		
Gafrarium pectinatum	5-15		
Gafrarium tumidum	5-10		
Isognomon ephippium	*		

Cephalopods:

Octopus	10-50	*Loligo* sp.	
Abralia armata		*Loligo edulis*	
Eutheuthis bartschi		*Sepioteuthis lessoniana*	
Loligo duvaucelli		*Sepia esculenta*	

Brachiopods:

Lingula sp.	1

Holothurians:

Actinopyga echinites	5	*Holothuria scabra*	5-30
Actinopyga miliaris	5	*Stichopus variegatus*	5
Bohadschia argus	10	*Thelenota* sp.	5-10
Holothuria atra	5-10		

Echinoids:

Echinothrix calamaris	1	*Tripneustes gratilla*	20-100

mainly of shrimp, while that from fish pots is almost exclusively crab. Beach seines and spears are used for squid and cuttlefish which are also occasionally caught with longlines.

No port sampling data is available for hand dredges and scissor nets. The former is used in seagrass beds to collect small gastropods for shellcraft, and the latter is operated off mangrove stands to take sergestid shrimps and milkfish fry.

Table 2 shows the average daily per capita catch of hand-gathered species which is a poorly monitored component of the overall fishery. Gleaners in intertidal areas are mostly women and children working in family groups who collect shells plus other edible or marketable species including small fish, crabs and seaweed. Hookah apparatus is used in waters up to 75 m deep to gather shells although this device is more often used to collect fish after blasting, an illegal activity.

Catches — Most species, especially shelled molluscs and echinoderms, are taken throughout the fishing season, although peak periods occur. Ferrer et al. (1985) report averages of 46 and 27 man-hours of fishing per week during high- and low-catch periods, respectively, over a 187-d annual fishing season in the Gulf. Peak

TABLE 3. Average daily catch of fishing gear in Lingayen Gulf, based on port sampling, 1983. C. = commercial; M. = municipal.

Species group	Lift Net		C. Trawl		M. Trawl		Fish Pen		Fish Pot		Beach Seine		Spear		Gill Net		Longline		Handling	
	kg	%	kg	%	kg	%	kg	%	kg	%	kg	%	kg	%	kg	%	kg	%	kg	%
Fish	16.0	43	289.5	96	5.6	37	7.0	51	5.4	54	9.5	84	6.1	77	10.9	94	9.3	95	10.0	100
Crabs	0	0	1.3	1	1.0	7	2.0	14	4.6	46	0	0	0	0	0.3	3	0	0	0	0
Shrimps and prawns	21.6	57	1.5	1	6.3	42	3.6	26	0.1	1	0	0	0	0	0.3	3	0	0	0	0
Lobsters	0	0	0.1	1	0	0	0	0	0	0	0	0	0.1	1	0.1	1	0	0	0	0
Sea mantis	0	0	0.2	1	0.3	2	0	0	0	0	0	0	0	0	0.1	1	0	0	0	0
Scallops	0	0	3.2	1+	1.8	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Squid and cuttlefish	0	0	4.3	1+	0.1	1	1.2	9	0	0	1.8	16	1.4	18	0	0	0.5	5	0	0
Octopus	0	0	0.1	1	0	0	0	0	0	0	0	0	0.3	4	0	0	0	0	0	0
Total	37.6		300.0		15.0		13.8		10.0		11.3		7.8		11.6		9.8		10.0	
Invertebrate component	21.6	57	10.5	4	9.4	63	6.8	49	4.6	46	1.8	16	1.7	23	0.7	6	0.5	5	0	0

fishing seasons in different sections of the Gulf coincide with periods when waters are calm, making it unclear whether high landings reflect greater abundance or more expended effort, since fishermen fish more often and longer per day under such conditions. This is especially true for intertidal species. Some gleaners have suggested that low catches during the wet season are due to reduced effort rather than to reduced stock abundance.

A number of populations, especially those of molluscs and echinoderms, may have decreased over the past 10 yr, based on declines in catch per unit of effort. However, it is not known whether this decline is due to reduced abundance or to an increase in the number of fishermen, or both.

In Table 4, official catch statistics (column A) are compared with estimates of annual catch (column G) derived from recall interviews (column B) and from port sampling (columns C–F). Official reports are known to be underestimates because an unknown portion of the catch does not reach the landing sites monitored by fishery enumerators. In addition, catches of most hand-gathered species are not quantified. Estimates from recall interviews are more realistic although these would also be low since the contribution of children, whose daily collecting activity in intertidal zones is considerable, could not be quantified. Catches of a few species in some villages for which the required information was incomplete were also not included.

Catches from municipal gear (columns C–D) are based on data collected from September to October. Thus species abundant only during this period (e.g., scallops) might be overestimated while those with peak seasons earlier in the year (e.g., squid) would be underestimated. While these may compensate for each other in the computation of total catch, the estimate is low since gear censusing was conducted in only 9 towns, and at least one group, sergestid shrimps, is unaccounted for.

Since estimates in columns B and E, Table 4, are assumed to be low, the higher value for each species group in the two columns was added to that for the commercial fishery (column F) to yield a better approximation of the total invertebrate catch from the Gulf (column G).

Official statistics cover only 6 species groups, catches of which were estimated in this survey to be actually 8% higher due to a larger landing in the "other bivalves" grouping. Species groups for which the official catch was reportedly negligible comprise 57% of the estimated actual total catch (approximately 1590 t, including mollusc shells but excluding sea urchins). The 2811 t total actual catch estimate from this survey is more than 100% higher than the official catch report.

In terms of value, the total catch would have been worth about ₱23 million, of which shrimps and prawns account for 52% and cephalopods 21%. Species groups not covered by official reports are valued at ₱3.2 million, 14% of the total value.

Catch per unit area — Average invertebrate catches over the entire Gulf using the above estimates would

TABLE 4. Annual invertebrate catch (t) and value (Phil. (P[a]) estimates for Lingayen Gulf, 1983. (A) Total 1981 catch, from *Fisheries Statistics of the Philippines*, vol. 31 (BFAR 1981); (B) Municipal catches, including hand-gathering, based on recall interviews; (C) Municipal trawl catches, based on port sampling; (D) Catches from other municipal gear, excluding hand-gathering, based on port sampling; (E) Total catch from municipal gear, excluding hand-gathering, from (C) and (D); (F) Commercial trawl catches, based on port sampling; (G) Total catch (commercial + municipal) using municipal values from (B) or (E), whichever is higher; (H) Estimated value of total catch based on 1983 prices.

Species group	A	B	C	D	E	F	G	H
Crabs	61	64	45	26	71	5	76	933 400
Lobsters	24	0.5	0	1	1	0.1	1	38 400
Shrimps & Prawns	326	154	284	17	301	8	309	25 769 400
Mantis Shrimps	1	27	14	1	15	1	28	353 200
Gastropods	—[b]	532	0	0	0	0	532	699 600
Oysters	—	839	0	0	0	0	839	1 092 000
Scallops	—	31	108	0	108	12	121	4 677 200
Other bivalves	10	300	0	0	0	0	300	301 600
Cephalopods	713	490	1	10	11	15	505	5 092 300
Sea cucumbers	—	100	0	0	0	0	100	267 000
Total	1135	2538	452	55	507	42	2811	39 224 100

[a] \$1.00 U.S. = Phil. P8.00 as of 1983

[b] Indicates negligible catches.

be 1.4 $t{\cdot}km^{-2}{\cdot}yr^{-1}$. The area of the Gulf within the 37 m isobath is roughly 850 km^2. Assuming that municipal fisheries are limited within this area and that commercial vessels operate outside it, annual catches would be 3.3 $t{\cdot}km^{-2}$ for municipal fisheries and 0.04 $t{\cdot}km^{-2}$ for commercial fisheries.

Hand-gathered species, which comprise 52% of the invertebrate catch, are taken largely within the 2 m isobath. Assuming a constant gradient within the 10 m isobath, which has an area of about 300 km^2, the area within 2 m would be about 60 km^2. Taking a figure of 70 km^2 to compensate for the more gradual slope towards the shoreline, the annual catch of hand-gathered species (gastropods, bivalves, octopus, echinoderms) would average at least 25.3 $t{\cdot}km^{-2}$.

Discussion

This survey provides the first realistic estimate of the magnitude of the unmonitored hand-gathering fisheries for molluscs and echinoderms at Lingayen Gulf. Although recall interviews are not the best means of acquiring catch data, catch etimates for other species groups obtained from interviews are comparable with those from port sampling data (columns B and E, respectively, in Table 4), at least on an order of magnitude basis. Differences between estimates from the two methods exist only for scallops, which are higher based on port sampling since this was done during the peak season, and for cephalopods, the estimate for which is higher from interview data due to the inclusion of octopus taken by hand. The catch estimate for hand-gathered species relative to other invertebrates is thus realistic.

Because of the magnitude of the hand-gathered catch, closer monitoring in the future is required. It appears that present catch rates have been sustainable because of (1) the high reproductive capacity of the target organisms, most tropical species being known to reproduce throughout the year; (2) the seasonal nature of the export market and a very minimal local demand, in the case of echinoderms; and (3) flexibility in raw material requirements in terms of species used in shellcraft, in the case of molluscs, allowing for substitution of one species for another depending on availability. However, since this is basically an open-access fishery requiring practically no capital costs, effort is difficult to control and ecological overfishing *sensu* Pauly (1979) may eventually occur.

In this regard, community-managed refuge areas for invertebrates as well as fish appear to be necessary to successfully impose size limits or catch quotas, as experienced by the Bureau of Fisheries (R. Miclat, BFAR, pers. comm.). A sense of powerlessness over the activities of others prevails among municipal fishermen, contributing to the tendency to take as much as can be caught despite a cognizance of the need to maintain breeding populations within their fishing grounds (M. Pagaduan, UP Institute of Social Work & Community Development, pers. comm.). Where BFAR has established artificial reefs under village control, however, it seems that what amounts to the granting of territorial use rights to the community has increased fishermen's receptiveness to conservation measures.

Catch Trends — No information except for annual catch records since 1976 exists for determining stock status for any invertebrate group or species in the Gulf. Total effort is not quantified but it is safe to assume that it is increasing. In this light, annual catch records may be indicative of total fishable biomass, and in the case of the more selective municipal fisheries, of fishable biomass of individual species groups. These show a drastic decrease in total fish and invertebrate landings after 1976, with 1981 landings being only 52% of 1976 landings. However, invertebrate catches were near the 1976 level in 1979 because of increased squid and shrimp landings.

In the Gulf of Thailand, greater squid and shrimp biomass associated with a reduction in fish stocks has been attributed to the removal of fish competing with or preying upon the latter (Pauly 1979 and 1982a). This is probably also occurring in Lingayen Gulf but has yet to be verified.

Comparing yield per area as suggested by various workers (ACMRR 1983; Gulland 1983; Marshall 1983) is not very conclusive, especially in the absence of effort data. For intensively fished coral reefs around Tutuila, American Samoa, Wass (1983) estimated a total annual fishery catch of 26.6 $t{\cdot}km^{-2}$ within the 8 m isobath, 32% of which consisted of invertebrates. This was equivalent to an annual invertebrate catch of 8.5 $t{\cdot}km^{-2}$ within that zone. For the 37 m isobath, a total annual catch of 4.7 $t{\cdot}km^{-2}$ was estimated, of which 1.5 $t{\cdot}km^{-2}$ consisted of invertebrates. While this value is less than half that suggested for the same depth zone in Lingayen Gulf, in neither area is there an indication of what fraction of the potential yield current catches represent. Also, the two areas are not strictly comparable since Tutuila is a reef system while the gulf includes a large percentage of soft bottom.

In San Miguel Bay, a trawling ground on the Pacific coast of Luzon, squid, crab and penaeid shrimp catches average 2.1 $t{\cdot}km^{-2}{\cdot}yr^{-1}$ (Pauly, 1982b, Table 4). Catches of these groups in Lingayen Gulf average only 0.4 $t{\cdot}km^{-2}{\cdot}yr^{-1}$. Pauly suggested that the annual fish and invertebrate yield of 17.5 $t{\cdot}km^{-2}$ from San Miguel Bay could probably not be substantially increased.

Given the catch trend in Lingayen Gulf and fishermen's perceptions that little more can be taken from the area at present, it is difficult to conceive of yields approaching that reported for San Miguel Bay. "Intricate harvesting" at different trophic levels as a means of increasing catches from multispecies fisheries (Marten and Polovina 1982) has long been occurring in municipal fisheries of the Gulf, where traditional gears have been supplemented with modifications of introduced gear types (e.g., scaled-down otter trawls used inshore; use of hookah apparatus in conjunction with spear and blast fishing). Whether an optimum mix of gear types can theoretically increase total catches is unknown, but such a mix would be difficult to realize in practice due to the sheer number of fishermen involved. Controls on gleaning would be difficult to impose for the same reason.

Information Gaps — The present survey has demonstrated the diversity of species taken from the Gulf and the relative importance of different species groups in the catch. The inferred decline in fishable stocks requires verification and estimates of potential catch upon which management options may be based remain to be made.

Conventional controls on invertebrate fisheries require detailed long-term data series on catch per unit of effort, total catches of different species groups, and total effort per gear type, all of which do not exist. Problems associated with data acquisition for management of tropical multispecies stocks have been discussed by many authors (e.g. Gulland 1979; Marr 1982; Pauly 1982a; ACMRR 1983). A vast range of problems from insufficient manpower and support facilities to an ambiguity of management objectives, is encountered in the Philippines.

Alternatives to classic stock assessment methods in the absence of a data base have also been proposed (e.g., Saila and Roedel 1979; Pauly and Murphy 1982). However, it seems that until interactions among species stocks can be conveniently incorporated in present assessment models, they will not be sufficiently predictive to be of practical use in tropical multispecies fishery management. This is especially significant in the Philippines where research funds are severely limited and are generally not allocated to projects of a perceived academic nature.

In the meantime, considering that in much of the country very little is known about even what invertebrate species are fished, provision of the same type of information as presented here would be of use in identifying areas and resources that require closer monitoring by the Bureau of Fisheries. The method employed is relatively inexpensive and may be improved substantially at minimal cost with inclusion of more questions in the interview protocol.

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Population Structure and Growth of *Callinectes toxotes* Ordway, in Buenaventura Bay, Colombia

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Callinectes toxotes inhabits mangrove swamps of the Colombian low lands along the Pacific coast and is the basis of an artisanal fishery of social importance but low economic value. Annual production in the San Antonio River is estimated at 16 t.

Females are slightly smaller than males with maximum carapace widths (CW) of 193 and 210 mm, respectively. Maximum wet weight for females and males is 432 and 500 g, respectively. Females and males are immature at CW < 127 and < 99 mm respectively.

There can be as many as 11 molts·yr^{-1}. Although the intermold period is variable with CW ≤ 100 mm, it varies little from 36 d for crabs of larger sizes. Von-Bertalanffy growth parameters are presented, and the estimated age at recruitment (CW = 50 mm) is 4 mo. It is estimated that *C. toxotes* males and females take 1 yr to grow from 2.5 to 203 mm CW.

Le crabe *Callinectes toxotes* se rencontre dans la mangrove des basses terres de Colombie le long de la côte du Pacifique et est la base d'une pêche artisanale qui a de l'importance sur le plan social mais qui a une faible valeur économique. On évalue à 16 t la production annuelle dans la rivière San Antonio.

Les femelles sont un peu plus petites que les mâles, la largeur maximale de la carapace (LC) étant respectivement de 193 et 210 mm. Le poids humide maximal des femelles et des mâles est respectivement de 432 et de 500 g. Les femelles et les mâles sont immatures lorsque la largeur de la carapace est inférieure à 127 et à 99 mm respectivement.

Il peut y avoir jusqu'à 11 mues par année. Bien que la période de temps s'écoulant entre les mues soit variable lorsque la largeur de la carapace est inférieure ou égale à 100 mm, elle varie d'un peu moins de 36 jours pour les crabes de plus grande taille. On présente les paramètres de croissance de Von Bertalanffy et on évalue à 4 mois l'âge au moment du recrutement (LC = 50 mm). On croit que les carapaces des *C. toxotes* mâles et femelles prennent un an pour passer de 2,5 à 203 mm.

Introduction

Species of the genus *Callinectes* have a wide distribution in the western hemisphere, from New Jersey (USA) to Uruguay in the Atlantic and from southern California to northern Peru in the Pacific. The species *C. toxotes*, the mangrove blue crab, or "jaiba" is found only in the Pacific (Williams 1974), from the Sea of Cortes (Mexico) to Ecuador and northern Peru, primarily in mangrove swamps.

Along the Pacific low lands of Colombia *C. toxotes* supports an artisanal fishery of significant regional and social importance. As a first step in establishing optimal fisheries management policies for *C. toxotes* this report briefly describes the crab fishery, growth parameters and local seasonal movements of the crab on fishing grounds in Buenaventura Bay (3°5′N, 77°10′W).

Methods

Data were collected monthly from fishermen operating in the San Antonio River (Fig. 1) from February 1983 to March 1984. The San Antonio River is a channel 6–7 km long, 0.3–0.4 km wide, and 3–4 m deep at low tide, located on the eastern side of the bay along 3°53′N. Crabs are distributed throughout the bay although higher concentrations are usually present in the San Antonio River. Size, as maximum carapace width (CW: spine to spine) and length (CL: tip of frontal teeth to posterior margin), weight (W), and sex were recorded for all samples.

Sexual development was determined from gonadal size, presence of sperm in seminal receptacles and seminal vesicles. The following categories were established:

Females:
1. Juvenile: spermatheca rudimentary or empty.
2. adult: ovaries developing, full spermatheca.
3. ovaries fully developed, empty spermatheca.
4. spawned, ovigerous mass yellow.
5. ova recently hatched.

Males:
1. juvenile, abomen fused to cephalothorax.
2. adult, free abdomen, seminal vesicles developing.
3. free abdomen, seminal vesicles full.

Growth rates were determined by holding three juvenile males and six juvenile females in a recirculating sea water system. Initial sizes were about 35 mm CL. Sea water was changed monthly. Maximum duration of holding was 150 d. Each animal was maintained

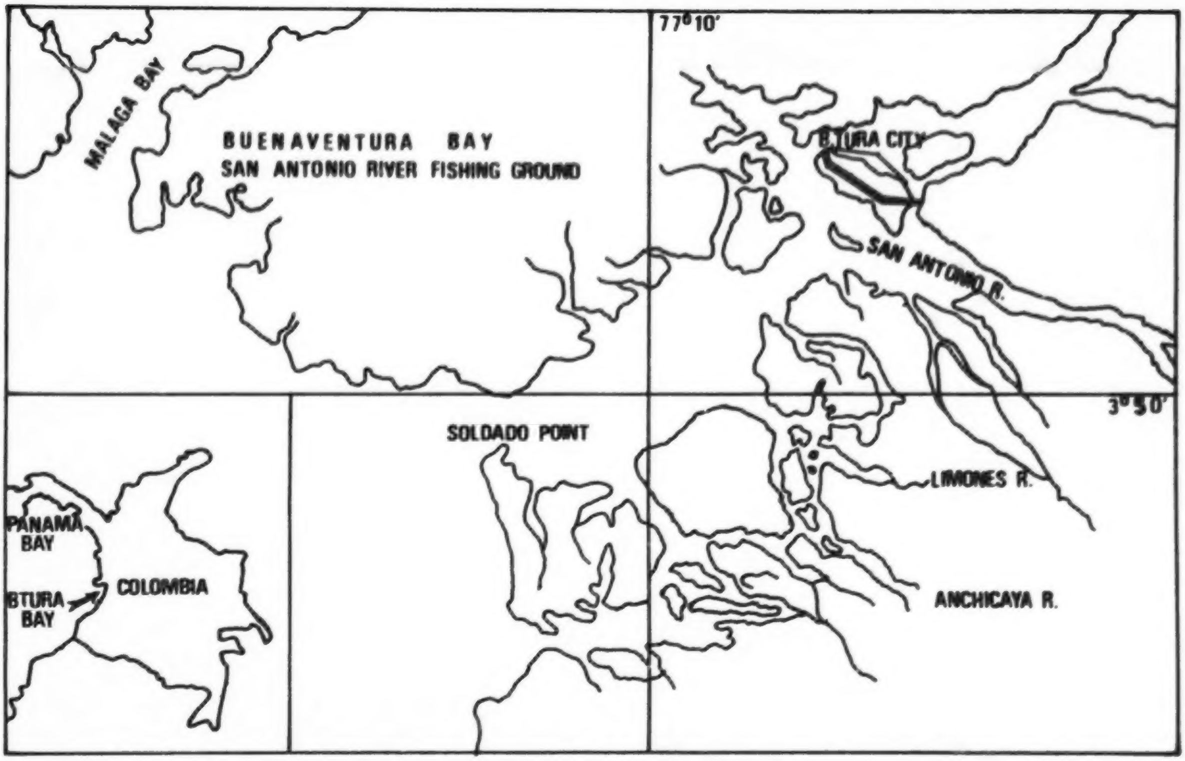

FIG. 1 Geographical location of Buenaventura Bay, Malaga Bay and the San Antonio River, in Colombia.

in a separate aquarium at room temperature (27°C) and at a salinity of 12–16‰. These conditions were similar to those found on local fishing grounds, where mean water temperature and salinity show little variation with slightly higher values (29–30°C; 16–20‰) during the first quarter, and slightly lower values (27–28°C; 12‰) the rest of the year. However, daily variations in salinity are far more extreme with values close to 16‰ during rising tides and as low as 0–2‰ at low tides. Dissolved oxygen is always high at the surface, with 6.25 mL/L as a mean for the whole estuary.

Crabs were fed fresh fish at a rate of 15% their biomass every other day. Food remains were filtered out after feeding to avoid fouling. The frequency of molting and growth increments per molt were recorded and used to estimate asymptotic carapace width (CW_{∞}) and growth factor (K) according to the Gulland and Holt (1959) method.

The Fishery

Many fishing communities are scattered along the coast exploiting the crab resource. Among these, the most productive are found at Saija, Timbiquí, Guapi, Guafuí, and Buenaventura. A reliable estimate of the number of full-time crab fishermen is not available. McMullen et al. (1981) estimated a total of 60–70 for the whole area from Buenaventura south to Guapi. Sporadic counting in the San Antonio River showed up to 20 dug-out canoes engaged in active crabbing. However, crabbing may sporadically involve the children, making a census still more unreliable. The total number of full-time crab fishermen can be much higher than McMullen et al. (1981) estimated.

Crab fishing as practiced today takes advantage of tidal currents to reduce paddling effort to and from the fishing ground. Thus, crabbing lasts from the first three hours of flooding to the first three of ebbing, totaling approximately 6 h daily. This time was used as a mean for production estimates presented in this report.

Crabs are usually fished with a variable length trotline baited with cow's lip or fish. Baited lines are laid on the bottom and after approximately thirty minutes are brought up carefully to the surface. Feeding crabs hanging from the line are scooped up with a hand net. These are deposited in a basket and covered with mangrove leaves to avoid desiccation until brought to the local market. Some of the catch is used by the family and surplus is boiled and iced for future use.

Crab production in the San Antonio River is variable over the year. The period from February to June with a mean production around 600 $g \cdot h^{-1} \cdot man^{-1}$, is followed by a decline in July–August (300 $g \cdot h^{-1} \cdot man^{-1}$). Production then increases to a maximum in November (1 120 $g \cdot h^{-1} \cdot man^{-1}$) to decline again in December–January to a figure around 500 $g \cdot h^{-1} \cdot man^{-1}$. The estimated mean catch$\cdot man^{-1} \cdot d^{-1}$ is 4 274 g. Weather conditions and other occupations reduce monthly fishing time to approximately 16 d. Total production per month is estimated at 68 384 $g \cdot man^{-1}$ or 151 $lb \cdot man^{-1}$. On the basis of 20 full-time fishermen for the San Antonio River, the estimated monthly production is 1368 kg or

16.4 $t \cdot yr^{-1}$. McMullen et al. (1981) estimated the crab production for the whole coast at about 80 $t \cdot yr^{-1}$.

Crabs are marketed by size rather than weight. The minimum size crab found on the fishing ground and retained by fishermen was 50 mm CW. During the good season a fisherman can capture up to 50 animals per day. The wholesale value of this catch may be up to \$1400 (Colombian pesos) or approximately U.S. \$10$\cdot d^{-1}$. Thus crabbing in the San Antonio River is a subsistence operation which does not generate an economic surplus.

Besides limitations imposed by technical drawbacks, several factors hinder expansion of the fishery. Pots, considered more productive elsewhere, cannot be used effectively because of the soft substrate of mangrove channels. Dredging has not yet been tested and conflicts with the shrimp fishery may arise since it could destroy shrimp nursery grounds. The most important limiting factors, however, could be infrastructural. In areas other than Buenaventura, increased production is limited by onland cold storage capacity, lack of processing capability and reliable transport to market centered in Buenaventura, Cali and Bogota. Opportunities for exporting are limited but price in the domestic market may justify landings up to 100 $t \cdot yr^{-1}$.

Morphometry and Sexual Development

As is characteristic of the genus, females are slightly smaller than males. In females, maximum CL was 91.6 mm, maximum CW was 192.6 mm and maximum weight (W) was 432 g. Relative weight of the ovaries expressed as percent of total body weight was a maximum of 24%. At CW < 127 mm, 100% of the females were immature. With CW = 137 to 161 mm, 61% of females had fully developed ovaries; 6% had extruded eggs. At CW > 155 mm, 85% of females were sexually mature (Table 1).

Maximum CL for males was 100 mm, maximum CW was 210 mm and maximum W was 500 g, though animals of this size were rare. Maximum testes weight was 9% of total body weight. At CW < 99 mm, 100% of the males were immature. At CW = 102 to 126 mm, 50% of males were immature with the abdomen still fused to the cephalothorax while 50% had a free abdomen and developing seminal vesicles (Table 1). Observations of mating in both the field and laboratory have shown that bigger males are more successful at mating than smaller ones, which are usually dislodged from the female through aggressive interaction.

Our data on size and sexual development suggest that females spawn more than once. First spawning seems to occur around a CW = 140 mm, and a second one around CW = 170 mm. The pleopods in egg-carrying females are more developed and hairy than in ungravid animals. After hatching, the pleopods hang below the abdomen and are prone to collect black sediment because the abdomen no longer fits tightly to the ventral surface of the cephalothorax. Females with these characteristics were captured outside Buenaventura Bay in July–August. Dissection showed developing ova in the ovaries, suggesting the occurrence of a second spawning. The spermatheca were empty, suggesting that molting and subsequent mating would be required for further reproductive success.

Equations relating W and CW for males and females, respectively, are:

$$\ln W = -7.442 + 2.554 \ln CW \qquad (r^2 = 0.8888)$$

$$\ln W = -7.162 + 2.471 \ln CW \qquad (r^2 = 0.9233)$$

Beyond CW = 160 mm, W is quite variable for females.

Population Structure

During March–April the male population is dominated by juveniles and in May–June by mature males (CW ≥ 126 mm). During the former period, the structure of the female population is dominated by larger individuals in the process of developing ova. In June the situation changes with a shift toward smaller females of CW ≤ 110 mm. This shifting of the population structure appears to be due to migration of larger females out of the estuary to spawn. Samples collected from outside Buenaventura Bay in July and August were dominated by large sexually mature and/or ovigerous individuals. The above pattern of growth, sexual maturation, and migration influences the sex ratio which showed a strong male dominance in July and August in the estuary (Fig. 2).

Individuals recruited to the inshore population in July consisted almost exclusively of juveniles (CW ≤ 102 mm). The period August–December is characterized by a population with maturing gonads.

Growth Factor, Intermolt Period, and Molting Frequency

Our observations showed that confined animals performed differently with respect to growth, females especially being less tolerant to laboratory conditions. Data presented here correspond then to a group formed of three males and one female. The experimental mean percentage increase in size per molt (% Icw molt) was 23.8 with a range of 10.2–44.9. We believe that the equation % $Icw \cdot molt^{-1} = 63.93 - 0.2394\,CW$, ($r^2 = 0.6889$) describes the field situation since the estimated $CW_\infty = 221$ mm ($CW_{max}/0.95$) is close to the observed maximum CW for females (192.6 mm) and males (210 mm). This equation allowed us to interpolate the % $Icw \cdot molt^{-1}$ for animals of size CW = 12.5 to 192.5 mm (Table 2).

The intermolt period (IP) is variable for CW ≤ 100 mm; for CW > 100mm it is more stable with values close to 36 d (Fig. 3). The equation $Lg_{10}\,IP = 1.431 + 0.00077\,CW$ allowed us to estimate the intermolt period for CW = 12.5 to 192.5 mm for all size classes (Table 2). The experimental mean was 32 d, with a range of 17–44 d. Estimated accumulated time for growth from CW = 2.5 to CW = 202.5 mm is 325 d; making an allowance of 40 d for larval growth, it appears that *C. toxotes* in Buenaventura Bay takes about 1 yr from hatching to reach maximum size. Estimated age at recruitment (50 mm CW) is about 85 d following settlement, or 4 mo.

TABLE 1. Length (CL) and width (CW) of the cephalothorax, total fresh weight (W), weight of the gonads (W_g) and maturity stage (% of N), for female and male of *Callinectes toxotes* Ordway in Buenaventura Bay.

N	CL (mm)	CW (mm)	W (g)	Wg (%W)	Maturity Stage (See method)				
					1	2	3	4	5
		females					percent		
20	51-60	110-127	87-144	0	100	—	—	—	—
85	61-70	137-161	134-245	1-24	3	30	61	6	—
39	71-80	155-175	115-322	1-17	0	15	56	23	6
		males							
45	31-40	76-79	39-40	—	100		—		—
32	41-50	86-99	40-61	—	100		—		—
31	51-60	102-126	57-132	—	50	50			—
26	61-70	99-145	116-260	1-4	—	30	60		
13	71-80	124-178	230-363	9	—		100		

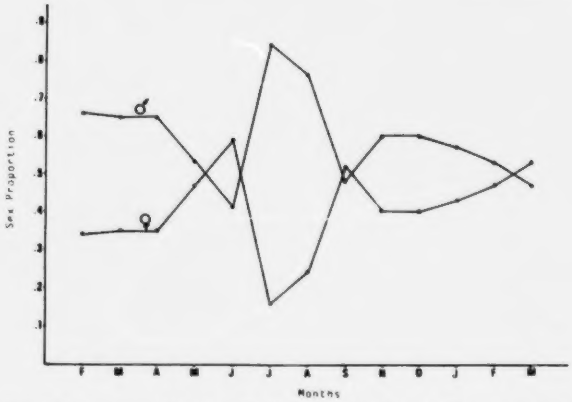

FIG. 2 Sex proportion for *Callinectes toxotes* in Buenaventura Bay from February 1983 to March 1984.

TABLE 2. Interpolated values between CW = 2.5 and 202.5 at 20 mm intervals for the percent increment in carapace width per molt (% Icw·molt^{-1}), intermolt period (IP), accumulated time for growth (t), rate of growth (% Icw·d^{-1}) of *Callinectes toxotes* held in a closed seawater system.

CW range (mm)	% Icw·molt^{-1}	IP (d)	Age (d)	% Icw·d^{-1}
2.5- 22.5	60.9	27.6	27.6	2.18
22.5- 42.5	56.4	28.6	56.2	1.99
42.5- 62.5	51.4	29.6	85.8	1.79
62.5- 82.5	46.6	30.7	116.5	1.60
82.5-102.5	41.8	31.8	148.3	1.40
102.5-122.5	37.0	32.9	181.2	1.21
122.5-142.5	32.2	34.1	215.3	1.01
142.5-162.5	27.4	35.4	250.7	0.82
162.5-182.5	22.6	36.6	287.3	0.63
182.5-202.5	17.9	37.9	325.2	0.43

[a]Excluding the larval period.

Mean growth rate (% Icw·d^{-1}) was 1.12, with % Icw·d^{-1} = 2.30 − 0.0097 CW. Slope of the regression line is equal to the growth coefficient (k) (Gulland and Holt 1959; Gulland 1969; Pauly 1983), k = 0.0097. Calculated on the basis of mean molt interval (32 d), k = 0.312. Intersection of the regression with the x-axis is an estimate of CW_∞ = 218 mm. A reliable estimate of t_0 cannot be obtained from our size-at-relative age data.

Discussion

Information collected from February 1983 until March 1984 allows some insight into the growth and reproductive biology of the San Antonio River population. Figures we have reported for CL and CW are well within the limits of those reported by Norse and Estevez (1977).

Because of their hard shell, mating in portunids occurs when a female's shell is soft following a molt, the only time she can be inseminated by a male. This behavior has been observed in *C. toxotes* both in the field and in aquaria. Mated females retain viable sperm in their seminal receptacles (spermatheca) until matu-

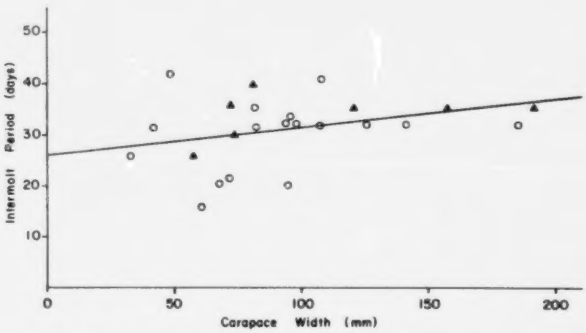

FIG. 3 The relationship between the intermolt period (IP: days) and the width of the cephalothorax (CW) for *Callinectes toxotes* males (▲) and females (○) held in a closed seawater system.

ration of the ova, which in this species can occur at 140 mm CW. The time required for egg hatching after extrusion is unknown in *C. toxotes*. DeVries et al. (1983a) reported a hatching time of eleven days in *C. arcuatus* from the Gulf of Nicoya, Costa Rica.

Information presented here on size and sexual maturity suggests that females can spawn at least twice during their lifetime. This is not unique for *Callinectes* species. DeVries et al. (1983b) reported that *C. sapidus* females can produce as many as three broods of eggs during their lifetimes. Protection for ovigerous females is not needed at this time since fishermen usually release them because of their low meat yield and poor flavor.

A reproductive migration by *C. toxotes* is inferred from the annual change in adult sex proportion and size frequency data. Similar movements are well documented in *C. sapidus* (Darnell 1959; Van Engel 1958; Tagatz 1968) and *C. arcuatus* (Paul 1982; DeVries et al. 1983b). From limited data, Norse and Estevez (1977) inferred seaward migration by females of *C. arcuatus* and *C. toxotes* along the Colombian coast. In *C. toxotes* migration to the spawning areas outside Buenaventura Bay seems to occur in July–August. During this period the area in front of Buenaventura is characterized by water of salinity higher than 27°/₀₀ suggesting similar higher salinity requirements for larval development as reported for *C. sapidus* (Costlow et al. 1959).

Callinectes toxotes had a mean molting frequency of 11 molts·yr^{-1} for animals between 2.5 and 202.5 mm CW. Van Engel (1958) reported 18–23 molts for animals of 2.5 mm CW to reach full size in *C. sapidus*, and Tagatz (1968) found that juvenile *C. sapidus* can reach harvestable size (120 mm CW) in 1 yr. It seems that *C. sapidus* in temperate waters needs a greater number of molts per year than *C. toxotes* to reach harvestable size.

In *C. sapidus* duration of intermolt was progressively longer with increasing size (Churchill 1919; Tagatz 1968). A similar relationship was found for *C. toxotes*. Mean increment in CW per molt found in *C. toxotes* was similar to that reported by Tagatz (1968) for *C. sapidus*.

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WORKSHOP SUMMARY

Research Advice and Its Application to Management of Invertebrate Resources: an Overview

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Jamieson, G. S., and J. F. Caddy. 1986. Research advice and its application to management of invertebrate resources, p. 416–424. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

Major issues relating to provision of research advice for conservation and management of invertebrate stocks are discussed. The considerable diversity of invertebrate resources has led to a variety of management approaches which have been generally categorized. Main regulatory measures discussed are size limits, quotas, and area/season closures (effort control). A requirement for managers to specify desirable objectives within overall fisheries guidelines, developed following discussion with fishermen and industry, is emphasized. Many invertebrate fisheries have made the transition from wild harvest exploitation to semi-cultivated or animal husbandry status, and wild stock enhancement options through the use of hatcheries, habitat improvement, and establishing resource sanctuaries are reviewed.

Approaches used in forecasting year-class strength are evaluated including, surveys, correlation of abundance with environmental factors, stock-recruit relationships, and biological interactions.

The importance of maintaining proper data bases for invertebrate fishery management was emphasized. It was recognized that the approach adopted often depends to a large extent on fishery status.

Criteria for establishing research priorities in the exploitation of invertebrate resources were considered. For developing fisheries, a project approach is often initially appropriate with transition to more routine monitoring and management procedures occurring as the fishery becomes more established.

Le présent document traite des questions importantes qui se rattachent à la fourniture de conseils en matière de recherche sur la conservation et la gestion des stocks d'invertébrés. La très grande variété des ressources d'invertébrés a donné lieu à différentes approches de gestion qui ont été généralement catégorisées. Les principales mesures de réglementation discutées sont: la limitation des tailles, le contingentement des prises et la délimitation des secteurs et des saisons (contrôle de l'effort de pêche). On y met l'accent sur l'obligation, pour les gestionnaires, de préciser des objectifs souhaitables respectant les directives globales des pêches, et qui ont été élaborés après consultation des pêcheurs et l'industrie. Nombre de pêches d'invertébrés sont passées de l'exploitation de stocks sauvages à la semi-culture ou à la gestion des stocks; on étudie les possibilités en matière de mise en valeur des stocks sauvages par l'entremise de piscicultures, de l'amélioration de l'habitat et de l'établissement de refuges.

Les méthodes utilisées pour prévoir l'importance des classes d'âge sont évaluées, notamment les relevés, la corrélation de l'abondance avec les facteurs environnementaux, les relations stock-recrue et les interactions biologiques.

L'importance du maintien de bases de données adéquates pour la gestion de la pêche d'invertébrés est soulignée. On reconnaît que l'approche adoptée dépend souvent en grande partie du type de pêche.

On considère les critères permettant de déterminer les priorités en matière de recherche sur l'exploitation des ressources d'invertébrés. Pour développer une pêche, il est souvent plus approprié de lancer tout d'abord un projet et d'adopter progressivement des procédures plus systématiques de surveillance et de gestion au fur et à mesure que la pêche se développe.

Introduction

As discussed in the overall introduction to this publication, the Workshop had two major purposes, 1) to provide a review of present approaches to stock assessment and management of invertebrates, and 2) to promote discussion of problems and identify useful priorities in developing biological research-based management strategies for invertebrate resources. While individual manuscripts addressed certain elements of the above, these issues were more specifically discussed in the last session of the Workshop by five working groups chaired by:

J. Reeves (Seattle, Washington), Application of conventional management approaches;

F. Serchuk (Woods Hole, Massachusetts), Recruitment studies and forecasting year class strength;

H. H. Haskin (Piscataway, New Jersey), Invertebrate stock enhancement;

J. Boutillier (Nanaimo, British Columbia), Managing data bases; and

R. C. A. Bannister (Lowestoft, England), Level of research investment vs. fishery returns.

Each of these working groups addressed the specific subject area indicated and met for several hours, after which their discussions were summarized by the chairman. What follows is our personal overview and perspective of these discussions, prepared after conclusion of the workshop from reports prepared by each chairman.

Application of Conventional Management Approaches

A necessary consideration in providing useful biological advice to managers is a thorough understanding of the effectiveness of traditional regulatory methodologies. These traditional approaches include size limits, catch and/or effort limitations, and time and/or area closures. Discussion focused on evaluating use of regulations where the main objective was to promote conservation of invertebrate stocks, rather than for economic and/or social considerations. The latter considerations are recognized as important but were not considered in detail during the Workshop. Conservation was defined as having three components: protection of reproductive potential by reducing fishery mortality on adults of a given stock, control of fishing effort on that portion (mature or immature) available for exploitation and, improvement of juvenile survival and recruitment.

Commercially exploited invertebrates represent a highly diverse group. Life history, biology, harvesting, and cultivation methodologies are often species specific. The general application of specific management strategies is often difficult to effect with acceptable results. As a result of this diversity, and until recently because of a general lack of communication on the effectiveness of alternate resource management strategies, past management practises for invertebrate resources have developed largely in isolation. Although management studies for various invertebrate stocks are obviously a fertile field for comparative study, conclusions on the desirability and consequences of management approaches are seldom stated.

One of the objectives of the Workshop was to begin identifying general categories within invertebrate fisheries where life histories and fishing strategies are sufficiently similar to permit a 'best' group of management strategies to be developed for each category. A preliminary attempt on the basis of species biology is in the last section of this paper. Other categories that might be appropriate and bear consideration could include trap fisheries for benthic crustaceans; manual gathering, including divers, of intertidal and subtidal molluscs, crustaceans and echinoderms; trawl fisheries for squid and shrimps; and gill and tangle net fisheries for squid and some crustacean species. Categorization, if proven useful, reduces the requirement to have to design management systems "from scratch" in each case.

In acknowledgement of the foregoing, any generalization attempted here regarding application of conventional management approaches must be taken in context. Nevertheless, several more commonly used management measures merit mention: size limits, quotas, effort control, and experimental management.

SIZE LIMITS

Minimum size regulations are among the oldest regulations enforced. They are justified to protect the reproductive capacity of the stock, even if a clear stock-recruit relationship is not known, and/or to restrict harvest of size categories to those sizes most amenable to processing or market demand. The importance of the former justification has grown over the last few years, because effective control of effort as a means of limiting catch has often proven difficult.

In many fisheries, minimal size limits are based on economic factors and were initially determined at a time when demand was lower and abundance and average exploited size were higher than at present. There if often, even today, insufficient biological information to support one particular minimum size over a lower or higher one. These economically determined size limits are now integral to many invertebrate fisheries, and while perhaps suboptimal, may nevertheless play a major role in protecting a resource from excessive overfishing. Some important fisheries [e.g. American lobster (*Homarus americanus*), Dungeness crab (*Cancer magister*)] have remained productive over a long period of time with only a minimum size limit as the main conservation measure. A specific size limit has proven amenable to enforce and often seems a fairly effective conservation measure, particularly if set above the size of first sexual maturity.

Despite the above, the setting of appropriate size limits alone should not be regarded as guaranteeing appropriate harvest rates under conditions of widely varying annual recruitment or harvest. It may be potentially unsuitable following major population decline. In those situations where a size limit is based largely on market criteria, there is a need to assess the danger of recruitment overfishing, particularly if effort has recently increased or stock abundance decreased significantly.

A size limit can have as its basis a yield per recruit analysis. Such a calculation is a useful first step as it balances rates of growth and mortality for the population, thereby providing a framework for determining appropriate size at first capture to achieve the highest yield for a given number of recruits entering the fishery. However, a lower rate of fishing than that giving a maximum yield is now generally considered desirable from an economic and stock-recruit perspective. With many finfish stocks for example, a lower rate of harvesting, such as that corresponding to $F_{0.1}$, is now widely accepted as safer and more desirable.

Many invertebrate populations tend to show frequent, large fluctuations in abundance, especially under high levels of exploitation and where the recruited population consists of only a few year-classes. In such situations where the equilibrium assumptions of many fisheries models are not met, yield-per-recruit calculations may prove misleading, since the one thing not taken into account, recruitment, is the controlling variable. Reproductive status is a principal concern with many populations and so a minimum size limit based on yield-per-recruit calculations alone, should be treated with some caution. Changes in population age structure caused by intensive size-selective fishing, such as a reduction in the age classes effectively supporting the fishery, may also make the populations less stable. Finally, even if the stock–recruit relationship is unknown, it is frequently useful to carry out calculations of fecundity per recruit for alternate management strategies to estimate what potential impacts regulation changes may have on population fecundity. Results from such analyses can be compared with results from yield-per-recruit calculations.

QUOTAS

Direct regulation of catch limits (by fishing unit, day, trip or season) is used in a number of invertebrate fisheries. For example, the simplest approach, a bag limit (e.g. number of clams per day), is applied to many intertidal mollusc fisheries. However, regulation by fishing unit alone is not an all-encompassing management technque in that it provides no overall control of landings in situations when number of participants in the fishery is increasing, and should be distinguished from quota (active) management *per se*, where annual landings (sometimes broken down by season, subarea or fleet component, or even to individual vessels in an extreme case) are specified in regulations in order to meet stated management objectives.

Although allocation between competing fleets is not addressed here in detail, it can be a major problem with a quota approach. Quotas also require more timely monitoring of landings data than do such passive management measures such as size limits and area closures, which essentially remain unchanged from year to year. Different theoretical targets may be the goal of quota management, such as attaining a specified fishing mortality rate or maintaining a predetermined minimum population biomass. These should be clearly specified, and monitoring of the fishery should be supplemented by some method of recruitment monitoring, especially if exploitation rates are high.

Good liaison with fishermen, and effective, timely enforcement and statistical monitoring are obvious preconditions for this management approach. Although the setting and enforcement of quotas pose problems, such as those caused by competition in the absence of vessel allocation and the resulting possible market disruption, from a biological perspective, the most serious problem is that considerable resources can be absorbed in simply collecting, updating and analyzing routine stock status data. This often leaves little research time to undertake fundamental biological study of the resource and its exploitation.

EFFORT CONTROL

Many invertebrate fisheries operate under effort control, which theoretically at least, would seem to reduce the requirement for the continual fine-tuning necessary with catch quotas because of natural fluctuations in abundance. With effort level predetermined, catch should fluctuate on the basis of availability of the resource. With effort control on an annual basis or long-term basis, the fleet fishing power is typically set to achieve a desired level of fishing mortality for some specific average population size, while recognizing that annual landings may fluctuate significantly around a mean. The experience here, as discussed in the fairly extensive literature on effort control and limited entry, has shown that a number of significant practical problems will arise. From a management perspective, the more serious of these relate to changes in fishing power of the fleet with time, such as the existence of "latent," or temporarily unused, fishing effort in the fleet at the time effort levels were set, and concomitant or separate changes in availability of the resource. From an industry perspective, resultant fluctuations in supply can cause problems in employment and financial return. Nevertheless, as one of a combination of tools for managing shellfish resources, this strategy has a great deal to recommend it.

Finally, it should be noted that allocation of fishing area, as well as catch, can be a concern. For example, as resource enhancement/cultivation becomes more widespread and successful, pressure to restrict parts of the productive environment to exploitation by specific user groups may become intense. This is practised already on an individual basis in a number of shellfish fisheries, both with explicit legal rights involved (e.g. oyster leases) and by common usage, as with some lobster fisheries. Conflict can arise particularly when traditional fishing patterns are disrupted by such activity.

EXPERIMENTAL MANAGEMENT STRATEGIES

Probing, or experimental, management was suggested as a useful approach in situations when little or no information is available on stock dynamics. An example is the establishment of a protective quota at what is believed to be a safe level, then modifying it over a sufficient time period to allow responses of the stock to be monitored. Such probing of the response of fishery systems to perturbations should lead to a better understanding of the consequences of different management actions, but to be effective, it requires a long-term perspective. Such an approach is probably only practical with newly developing fisheries or with species that are distributed in numerous, geographically isolated populations where a "controlled" or comparative approach to yield modelling may be possible. Experimental management implies that suboptimal, but still "safe", management will occur over the short term. When fishermen's incomes are involved, opportunities for such manipulation of stock yields for purely research purposes may be greatly restricted.

With respect to initial establishment of conservative management measures in the early stages of fishery development, attention was drawn to rapid advances in the area of "short-cut" assessment theory and its application, especially for tropical fisheries. More work is needed in drawing up guidelines that would be useful for roughly establishing stock status and arriving at preliminary, conservative management measures.

In a more general discussion of management, two important interactive systems which merit close examination were identified. Firstly, it was generally recognized that economic factors are important and concern was expressed that the fundamental links between economic and biological management may still not be fully recognized and appreciated by scientists and managers. Economic considerations form the bottom line of most management situations, and must be included in any research analysis searching for optimal strategies. Although often implicitly considered in the development of management policy, socio-economic considerations must explicitly enter into management decision-making and should be resolved by discussions between economists and other experts in a common management forum before management policy is finalized. It was suggested that the general topic of bioeconomic interaction in management of invertebrate fisheries should form the subject of a future symposium.

The second interaction of concern deals with that between scientist and manager. Fishery scientists are frequently involved in providing advice to managers, and ideally such advice should take the form of a set of options and their likely consequences. It was generally felt that managers need a finer appreciation for the risks, or degree of confidence, associated with any given option, and that they should likewise clearly identify to scientific advisors the constraints imposed for legal, social, or economic reasons on the use of management alternatives available.

Finally, a more thorough retrospective evaluation of the consequences of past utilization, or even lack of utilization, or biological advice by fisheries managers is recommended.

Recruitment Studies and Forecasting Year-class Strength

Four major approaches to estimating or predicting year-class strength in invertebrate stocks were identified. These approaches, and representative examples of stocks where they have been applied, are:

FISHERY INDEPENDENT ESTIMATES OF RECRUITMENT BY DIRECT SAMPLING:

This is the prediction of recruitment based on direct measurement or empirical indices of prerecruit abundance. This is practical in some invertebrate fisheries, and involves either surveys or the routine use of larval or post-larval collectors. This type of methodology assumes that: (a) year-class strength has already been established for the prerecruit life stages being sampled, (b) a significant correlation exists between prerecruit abundance and subsequent recruitment to the fishery, and (c) sampling techniques consistently and reliably capture prerecruit stages in proportion to their abundance.

Examples presented at the workshop included research survey estimates of prerecruit abundance for sea scallops (*Placopecten magellanicus*), surf clams (*Spisula solidissima*), red king crab (*Paralithodes camtschatica*), Dungeness crab, tanner crab (*Chionoecetes* sp.) and the determination of puerulus settlement densities for New Zealand rock lobster (*Jasus edwardsii*).

CORRELATIONS BETWEEN RECRUITMENT SUCCESS AND ENVIRONMENTAL PARAMETERS

Prediction of recruitment success has occasionally been based on empirically-derived statistical relationships between abiotic factors (e.g. meteorological conditions, water temperature and other hydrographic factors) and subsequent abundance of recruited year-classes after they have passed through critical life-history stages under these conditions. This type of approach assumes that physical factors affect year-class strength, either through their effects on spawning success and/or survival of progeny, or that both the environmental variable used and recruitment success are together reacting to the same forcing variables. In each case, the correlation between physical factor values and resulting abundance must be high (i.e., the variables in question must explain enough of the total variance to be useful for predictive purposes). As implied, time lags will exist between environmental influence on year-class strength and resultant recruitment to the fishery, and a number of models of fishery production specifically use such lagged terms. To date, most predictions have been used in research studies of possible causal mechanisms rather than for management per se.

Examples presented at the workshop included correlations between water temperature and abundance (Dungeness crab, pandalid shrimp, American lobster) and tidal cycles and/or current patterns and abundance [blue crab (*Callinectes sapidus*) and sea scallop].

FISHERIES PRODUCTION AND STOCK AND RECRUITMENT STUDIES

Predictions of recruitment or expected fishery production can be based on analyses and models incorporating time series of catch, effort, and environmental variables and biotic factors, in various combinations. These methods in their simplest form are analyses of cross-correlation and/or autocorrelation of data in the time series. The relationships are empirical and do not necessarily reveal any causal processes between dependent and independent variables. Methods include surplus production models using both conventional effort data and biological indices, stock-recruitment relationships, Leslie/DeLury population estimation methods, and time series analyses. Each method possesses its characteristic data requirements, assumptions and constraints, some of which are discussed in preceding papers in this volume.

BIOLOGICAL INTERACTIONS

Biotic processes (predation, parasitism, competition, and cannibalism) can also impact on recruitment and abundance, and the extent of such interaction has been used to predict stock status. Approaches described include various empirically derived relationships between biological phenomena (e.g., abundance of predators, incidence of parasitism, etc.) and fluctuations in recruitment success. Recruitment variation is presumably mediated through changes in natural mortality, changes in reproductive output, inter- or intraspecific competition for settlement spaces and habitat, and/or behavioural modifications affecting survival and availability. In most cases, the causality and association of observed events have not been clearly resolved and the usefulness of these factors in improving prediction remains uncertain.

A) At what stage in the life history is the strength of year-classes determined, and is that invariant over time?

This was identified as a critical problem since the usefulness of prerecruitment sampling depends on the assumption that year-class strength has already been largely determined before sampling a specific life stage begins. More generally, any search for a relationship between abundance of different life stages, or between recruitment and biotic and/or abiotic variables, prior to establishment of year-class strength is unlikely to be successful.

B) What are the causal mechanisms determining year-class strength?

This was recognized as a critical study area since inclusion of relevant factors controlling year-class success is desirable within any predictive model. Although good predictive models do not have to be necessarily causal in nature, they shed more understanding on the underlying processes affecting production when they include causal factors. Delineation of causal factors, although often time-consuming and costly, provides a more substantive basis for fishery management policy and will influence sampling strategies and population models developed, particularly those aimed at explaining recruitment variability. This is especially true if environmental and ecological changes periodically disrupt perceived normal relationships.

C) What constitutes a sufficient time series of data for prediction of recruitment? How cost effective is acquisition and maintenance of such a time series, and how reliably and rapidly can predictions be validated?

These problems were identified as practical concerns significant to both scientists and fishery managers alike, although little general guidance on these matters could be offered. Relatively few long time series of invertebrate fishery and research data exist which could be used for recruitment prediction. Where there are such data the cost has been significant, particularly when research surveys have been used. In general, this expense has only been incurred in cases where landed value has been relatively large in comparison to costs of data acquisition (i.e., stocks producing millions of dollars of revenue annually). It is significant in this connection that regular research surveys are a common feature in management schemes of many finfish resources, but are less frequently used for invertebrate resources. This may in part be due to the relatively difficult and expensive sampling of invertebrates, arising because of their limited mobility and often cryptic behaviour in structurally complex, benthic habitats.

In providing forecasts to managers and industry, it is desirable to provide information as far ahead of recruitment to the fishery as possible in order to allow flexibility in developing appropriate responses. However, for most intensively exploited species, only a short time interval often exists between the time when empirical estimates of prerecruit abundance can be reliably derived and when recruitment occurs to the fishery. In contrast, for some long-lived, slow-growing species |e.g., ocean quahog (*Arctica islandica*), geoduck (*Panope abrupta*)| where a prolonged interval may exist between the time at which year-class strength is first establishable and when the cohort is first commercially exploited, this information may be less critical because of a general low annual recruitment and a large number of year classes in the exploitable population.

Problems in forecasting year-class strength can arise from 1) an incomplete knowledge of the resource being studied or managed, and 2) incorrect formulations of predictive recruitment models due to poor data collection, data quality and/or a limited understanding of system behaviour. In all cases, these shortcomings could possibly result in acceptance of a false understanding (Type II error) of the causal factors regulating year-class strength. This could lead to potentially serious management consequences if resulting advice was recommended and accepted.

Requirements for recruitment forecasting depend on the management system selected. For example, management in which an annual quota approach is used might require particularly accurate and timely recruitment forecasts, while size limits and seasonal controls of fishing might only require coarse or no forecasts of incoming recruitment. In the case of effort control, the use of a recruitment forecast is principally for economic purposes. Although many invertebrate fisheries are not managed in an "active" sense, information on recruitment is often useful to managers, since high exploitation means the recruited year class may be the main component of the catch. Variation in year-class strength may thus be the main factor affecting fluctuations in landings.

Recruitment dynamics between crustaceans and molluscs are likely different due to differences in life history patterns and behavioural characteristics, both between and within the two groups. The relatively larger amount of metabolic resources that most crustaceans invest in individual progeny as opposed to the broadcast spawning activities characteristic of many bivalves might suggest a greater population stability for the former, but it is far from clear if this generalization has any validity, especially for exploited stocks. Using minimum size and closed area restrictions to protect spawning individuals seems of a priori importance, but there are few derived relationships between spawning stock size and subsequent year-class strength for most invertebrates. Despite this lack of information, the consequences of assuming no stock–recruitment relationship when in fact one exists, could be severe. This is particularly important if population size is low. Accordingly, the use of minimum size regulations related to size and maturity, and seasonal/area closures, are considered to be conservative approaches and to be recommended, at least until a clearer idea of stock and recruitment relationships are available.

Invertebrate Stock Enhancement

Four possible approaches to enhancement of invertebrate populations are:

1. Use of hatcheries or nursery areas to enhance wild stocks.
2. Habitat improvement.
3. Establishment of sanctuaries or refuges.
4. Practise of husbandry techniques.

In general, the potential for enhancement of wild stocks of invertebrates has not been rigorously investigated in recent years from either a biological or an economic perspective.

USE OF HATCHERIES

Raising juveniles in hatcheries, and distributing them over extensive common property areas of natural habitat, is contrasted here to mariculture, which is defined as controlled production of animals for marketing under private ownership conditions. The long experience in eastern Canada and in New England of attempting to enhance natural American lobster stocks by use of hatcheries is an example. These hatcheries operated from the turn of the century to about the 1930s and 1940s; one hatchery in Massachusetts continues to operate. With lobsters, there has never been a clear demonstration that wild stocks have been increased through such releases (although in the absence of controlled observations and field experimentation, this was not expected). More critically, calculations made in the late 1940's indicated that the cost per juvenile of lobster released in Maine was about equivalent to the market value of a legal-sized lobster at that time, causing the program to be deemed not cost-effective.

Hatcheries have been used in Japan to produce juvenile abalone for enhancement of wild stocks, but to our knowledge there is no known published information that such enhancement has in fact contributed to higher fishery yields, or done so in a cost-effective way.

Oyster hatcheries operate in many countries, but most are devoted to mariculture rather than to enhancement of natural stocks. They could be used to provide seed for such enhancement, but the consensus of the group was that such enhancement would also not be cost-effective. There is a possible example of a wild oyster stock being enhanced as a spin-off to an oyster mariculture operation, but details are poorly documented. The Franklin Flower and Sons Oyster Company of Bayville, Long Island, operates a hatchery to produce seed for planting directly on growing grounds. Two years ago, a heavy natural set occurred over a wide area around these grounds and it has been suggested that this was due to the concentration of initially hatchery-produced adult stock, although as usual in these cases, information is circumstantial. A similar phenomenon followed culture of Mutsu Bay scallops in Japan.

Participants agreed that hatchery techniques may be useful in the future to aid development of selected strains for special situations, such as improved disease resistance, rapid growth, high meat yield and quality, and adaptation to particular habitats. Reservations were expressed, however, as to the effectiveness of such procedures in improving the characteristics of natural, local stocks. Introduced, improved strains may not dominate natural stocks genetically, and may not become established in any given area. If they did so, it is not clear that they would show the same response to environmental change as the local stock and although improved in one characteristic, they may not be preferred in others.

HABITAT IMPROVEMENT

This approach includes such approaches as pollution control, predator removal, substrate modification, and construction of artificial reefs.

The importance of protecting invertebrate stocks from toxic substances and pollutants is well recognized. Many invertebrates are sessile or have limited mobility, and cannot avoid pollution when it occurs. Pollution must be controlled, or in some situations, the animals may be relayed to cleaner water to produce a marketable product. It was recognized that in some instances the closure of areas to harvest because of sewage pollution may provide a sanctuary for brood stock, which may be important in maintaining populations in surrounding, unpolluted areas.

Predator control can take a variety of forms. It was suggested that the rebuilding of Alaska king crab stocks could be expedited by heavy fishing of cod, one of their suggested principal predators. Predator control is actively practised in oyster culture, e.g., mopping starfish, trapping drills, and using off-bottom culture to avoid predators, but these methods are generally easier to practise in mariculture than in the protection and enhancement of wild populations.

Improving substrates for enhancement of invertebrate stocks has been attempted in several instances: addition of oyster shell as "cultch" for attachment of larvae, spreading of gravel to provide habitat and protection for juvenile clams against their predators, and topographical modification of the sea floor to create bottom irregularities, have all been used to concentrate settlement of larval stages of various benthic species. Construction of artificial reefs has been extensively practised in Japan to enhance natural populations of a wide range of invertebrates, including abalone, sea urchins, and crustaceans, although cost-effectiveness of these approaches has rarely been documented.

ESTABLISHMENT OF SANCTUARIES

Sanctuaries or closed areas have been recommended and sometimes used for preservation of brood stock or protection of nursery areas and juveniles. There are serious gaps, however, in our knowledge of the life cycles of many commercially important invertebrate species, and the "critical" life stages at which year-class strength is primarily determined are largely unknown. Juvenile stages of many species appear to require specific "nursery" conditions, and if natural recruitment is to be increased, then it is essential that these "bottlenecks" be identified. Increasing production from nursery areas could eliminate or reduce some problems, and perhaps lead to enhancement of wild stocks.

Three approaches are available: (1) concentrate early life-stages in specific, controlled areas or seed beds, followed by transplantation to natural areas where various methods of husbandry are employed until harvest; (2) enhance production of overly dense, natural populations by "thinning", through controlled relaying or harvest; and (3) develop markets for smaller-sized, harvested animals.

Rack and tray culture of oysters in France and Australia and raft culture of oyster in Japan are well known examples of the first approach. There are economically viable culture techniques for other species such as clam culture in Asia, scallop culture in Japan, and mussel culture in Europe. Intensive culture operations will probably continue to expand throughout the world and be useful for increasing production of a variety of invertebrate species.

An example of the second approach is with oyster and mussel relaying. In some instances, however, such as with some surf clam populations off the United States east coast where relaying is not economically practical, populations are so dense that growth is limited and legal size may not normally be attained. A similar situation exists with some sea scallop populations, where either density and/or environmental conditions do not allow the realization of full growth potential. Harvest and processing of some sublegal size animals may be justified under such circumstances. Gourmet markets for smaller sizes of some species such as hard-shell clams have developed, and this approach has been considered by mariculturists for other invertebrates (e.g. lobster, abalone).

Finally, since both growth and survival are often size and density dependent, there should be a desirable size:density relationship which maximizes production and economic viability. Definition of optimal biological factors at the time of release should be integral to any relaying or enhancement operation.

Managing Data Bases

Establishment, updating and use of data bases for fisheries stock assessment and management are all ongoing concerns for most fisheries scientists. Basic problems are in clearly identifying what objectives are to be achieved, what type of data to collect and how much, and subsequently designing or modifying a system of analysis to achieve desired outputs in a timely, cost-effective, efficient manner.

Establishing a data base useful over the long-term is difficult since a fishery and its management are both dynamic systems which often change greatly with time. However, utility of a time series increases significantly with the number of years that it continues, and it is obviously important initially to spend sufficient time deciding which data should be collected. Two problems often exist: firstly, how to utilize existing sources of information optimally: if data series already exist, they were usually established for poorly defined or different reasons, may incorporate potential or sometimes known sources of bias and may be poorly structured or too expensive to update. Eliminating, if possible, such sources of bias can be a major task. From existing experience with data series, the question of how to optimally establish a framework for new data bases, when we do not always know what types of research and management questions will have to be answered in the future, is a continuing problem. Nevertheless, one conclusion is that starting new data series and termination of old ones should not be established in an ad hoc fashion in response to immediate needs.

Secondly, detailed biological knowledge of the species being managed is often lacking, making it difficult to establish critical life history periods, or "bottlenecks", for close monitoring before data collection is initiated. Traditionally however, three general types of data have been collected:

a) basic fisheries data (performance indicators, including commercial catch and effort),
b) biological data (growth rate, fecundity, mortality, etc.),
c) oceanographic data (temperature, salinity, current patterns, etc.).

While ideally this information should be collected for all fisheries, resources are generally limited, and priorities have to be established as to what information is most relevant and cost-effective to collect.

Concern was expressed about maintaining data quality versus quantity and the importance of documenting biological and fishery-related sampling procedures and their underlying assumptions. For example, morphometric conversion factors for size and/or weight, and accurate estimation of the percentage of total catch which goes unreported, are both mundane but vital concerns. Under the guise of a standardized procedure, it is easy to become "locked in" to a particular methodology or approach and not regularly test inherent assumptions. This often leads to subsequent difficulties in using existing data in new analyses. Alternatively, frequent "improvements" in sampling design may destroy the value of time series and their continuity.

The utility of completing log records, either on a voluntary or compulsory basis, and the relative value of logbooks in comparison with fishermen's interviews were also discussed. No general consensus was discernible, and it was concluded that optimal practice depends both on specifics of the fishery and on human and financial resources available for data collection.

A voluntary logbook or interview system gives high quality data, but close two-way communication with industry is required. The danger is that "volunteers" completing logbooks may not be typical of the population of fishermen as a whole. A compulsory logbook system generally gives poorer quality data, especially if fleet movement is regulated, but may require less manpower to maintain. The likelihood of significant errors being deliberately introduced exists, and may bias resulting analyses.

Since developed countries often have considerable financial and manpower resources for fisheries research and management, total census of a fishery is more common there than in lesser-developed countries where these resources are usually limited. This does not imply, however, that sampling schemes in developed countries are particularly cost-effective or free from bias. If data collection is standardized, and a suitable sampling design established and routinely evaluated, sampling can often be made more cost-effective yet still yield data of acceptable quality, and problems of bias can be dealt with in a more explicit fashion.

A potential conflict of interest may occur if managers, who establish regulations and ensure that they are effective, are also involved with the collection or analysis of fishery performance indicators. Confidentiality of research information from enforcement staff must be maintained if high quality data are to be achieved. Similarly, if the active involvement of fishermen in fishery management is solicited, it should be routinely explained to them how the data they provide are used to produce optimal management policy and/or resource conservation. The need for effective two-way communication between researchers and fishermen to ensure maximum cooperation was stressed.

Level of Research Investment vs. Fishery Return

Research managers need to reconcile requirements for routine monitoring and assessment activities (and data collection activities discussed earlier that support them) with requirements which allow a better understanding of resource biology and its interrelationship with environmental factors. This latter activity is often referred to as primary research. A third area competing for research resources relates to short-term, unanticipated "fire fighting" activities. Unless control is exercised, these may pre-empt or disrupt unnecessarily both other types of activities described above and might postpone a structurally sound response to long-term management problems. Ideally, research managers should be able to set aside a proportion of their "research" budget for each of these three purposes.

Research managers frequently encounter other types of problems in establishing research priorities, and in particular, in assigning limited resources between research to competing fisheries where political and social factors may differ in importance with time. Within each fishery, research priorities should be spelled out for each given species or research need, so as to resolve or optimize the "mix" of short and long term management strategies and the resolution of relevant biological questions.

At the outset it was noted that maximizing economic return from a fishery, and the presumed potential benefit of management, are not necessarily the most important criteria use in priorizing research budgets. It was also noted that the scientific value of research is often disproportionately high in the early stage of a fishery when economic value is least, particularly if this allows an early solution to management problems and heads off later, potential conflict. It is also conceivable that formerly valuable fisheries, which in themselves are now of low value, may be reestablished if significant effort is allocated to promote recovery. Other stocks may be of interest if their population trends give important signals about particular aspects of the overall biological system, making them worthy of study independent of their present economic value. This latter alternative may be a strategy that is only fully available to developed countries because of their generally larger commitment to fisheries research. Finally, as noted above, it should be understood that while monitoring programs may broadly give the status of stocks, we are now reaching the point with issues such as stock-recruitment relationships where further progress may only be made by increasing our general understanding of biological processes. Studies of such topics may involve programs which are large, relatively costly, and not always initially obviously fishery-related, causing traditional cost-benefit analyses to be a poor basis for evaluating their merit over the short term.

It was recognized that it may be difficult to match research resources to objectives, particularly in developing countries, where the highest priority may be finding quick solutions to pressing problems. This often leaves less room for developing a detailed understanding of the resource base. The consequences of following this short-term objective should be clearly stated by resource advisors, since it strongly influences the choice of management method and type of return achieved.

For a given fishery project, research costs will depend on chosen methodology, intensity and frequency of observation, and the geographical location of the resource. However, a fundamental underlying consideration is the biological characteristics of the population supporting the fishery. These have been used to characterize invertebrate fisheries into five categories:

1) Crustacean populations of nearshore, benthic (lobster) type.

These appear to be regularly renewable and seem to be generally stable following long-term extensive harvesting, often with only a minimum size limit and moderate effort restriction as regulations. General production models based on CPUE analyses, and analytical yield per recruit models based on length composition analysis, are effective approaches for making objective management decisions about both the consequences of different levels of exploitation and minimum size limits. However, these models do not predict recruitment and depend on assumptions about natural mortality. They also require regular monitoring of catch and effort data, sampling for population length frequency compositions, and tagging for growth data. Present uncertainties relate to the effect of environmental factors, habitat constraints and intra- and inter-specific competition on distribution, abundance and size composition; the degree of prerecruit density-dependence; factors affecting abundance and distribution of larvae for stock definition; and factors affecting efficiency and catchability of survey and fishing gear. It would seem cost effective to maintain monitoring programs generally, and to study these other factors on a project basis.

2) Crustacean populations of offshore, benthic (crab) type.

Some crab populations (e.g. *Cancer, Callinectes*) fall into the same general framework as lobsters, but other populations, notably those of some king crab and *Chionoectes* species, are sufficiently localized and their fisheries valuable enough to allow consideration of other assessment methodologies. For these populations, which are often managed with annually-assigned quotas, the most immediate return for research investment appears to lie with the use of surveys to assess population distribution and to measure and predict short-term abundance changes. This may be supported by modelling to adapt hypothesized population responses to environmental and/or biotic factors into a preliminary, predictive tool.

In the long term, it is important to determine the extent to which these generally new fisheries impact on population long-term stability, and this seems to justify specific study of the relationship between stock abundance, exploitation level, environmental factors, and subsequent recruitment.

3) Invertebrate populations of short-lived, mobile (squid, shrimp) type.

These include short-lived, often physically small species which demonstrate moderate-high mobility and relatively rapid fluctuations in perceived abundance. Abundance may be actually low, or may appear low because of dispersal of these relatively mobile individuals in response to various environmental features. These species are generally fished with trawls and must be concentrated in abundance to permit viable exploitation. Steady state yield modelling is often less appropriate and informative than are recent surveys aimed at measuring short-term abundance and distribution. Multivariate predictive modelling based on a range of environmental inputs and on predator prey interactions and surplus production modelling may also be effective.

4) Invertebrate populations of long-lived (scallop) type.

These include abalone, geoducks, ocean quahogs and some scallops and are relatively long-lived species (> 10 yr) which in some cases at least, have been exploited for decades. Aggregated yield models may give general guidelines for management, particularly in relation to minimum size. However, these relatively low-mobility species often show contagious distributions by size (age), so that effective fishery management seems to require an additional understanding of spatial dynamics. The best research investment is therefore likely to include a combination of abundance surveys, disaggregated models, and recruitment-oriented studies.

5) Invertebrate populations of short-lived, low-mobility (intertidal clams) type.

These populations are usually highly variable in abundance and distribution with large-scale, short-term fluctuations generated by irregular recruitment. Life spans are usually < 10 yr. Long-term sustained harvesting at specific locations may be difficult to achieve, so management may have little to contribute beyond thinning or spinning out populations depending on relative abundance, though leasing or rotational closures have been suggested as possibilities here. The main contribution from research in the short term will be to estimate short-term abundance and distribution using survey techniques (transects, grab surveys, dredge surveys). The scope for enhancing landings by planting hatchery-reared stock may be correspondingly much greater here. There are logistic advantages to ecological studies aimed at finding the causes of settlement variability, but from a short-term fishery management perspective, these are not a good investment.

Most fisheries research ultimately reaches the point where a decision has to be made between maintaining routine, conventional stock prediction and assessment programs based on surveys or simple aggregated yield models, and initiating larger-scale, more fundamental programs to achieve a rigorous understanding of the biology of the species and its interactions. This decision point usually comes when long-term predictive advice is solicited and knowledge about the stock-recruit relationship is required, or when limited participation in the fishery is being considered and scientific rationalization and justification is desired. Generally speaking, assessment approaches which only consider species' growth and natural mortality seem less desirable for invertebrates than for fish, since generally, for the majority of crustaceans and bivalve molluscs, environment and behavioural events seem to have a greater effect on spatial pattern of occurrance and resulting population dynamics. Greater biological understanding must be achieved if advice to managers is to be reliable over the long-term. This is the point where the level of investment versus fishery return is particularly hard to gauge.

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